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Proceedings of the Workshop on the Biology and Resource Potential of Cephalopods Melbourne, Australia 9-13 March 1981

Cover illustration:
Sepioloidea lineolata (Quoy & Gaimard, 1832) (Sepiadariidae: Cephalopoda), an Australian endemic species known to occur in the coastal waters around Australia, except the north coast. (Drawn by Rhyllis Plant from a photograph taken by Ian Kirwen).

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PROCEEDINGS OF THE WORKSHOP ON THE BIOLOGY AND RESOURCE POTENTIAL OF CEPHALOPODS MELBOURNE, AUSTRALIA 9-13 MARCH 1981

Workshop Organizers

C. C. Lu, J. Thompson, and Clyde F. E. Roper

Scientific Editors

Clyde F. E. Roper, C. C. Lu, and F. G. Hochberg

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FOREWORD

Like that of most top-level marine predators, the role of cephalopods in the biological economy of the sea is complex and our knowledge of it is fragmentary. Except for two or three species of squid and octopus almost nothing is known about cephalopod spawning and spawning grounds, duration of larval life, life span, age at maturity, fecundity, growth rates, population size, migrations and place in the food web. Yet, in recent years exploratory fishing has revealed that in many parts of the world's oceans, cephalopod populations comprise an immense exploitable food resource for mankind.

In 1945 the world-wide cephalopod fishery yielded 500 000 tonnes. The current annual production varies between 1 and 1.5 million tonnes and there are indications that the potential may be many times this if only we can learn more about the life of these animals.

Substantial squid resources are now known to occur within the Australian Fishing Zone, especially in Bass Strait and the North West Shelf. Our knowledge of these resources is so poor that some species being fished commercially remain unidentified, and at least one is un-named and undescribed in the scientific literature. Development of the Australian squid fishery is still by rule of thumb and lacks any degree of scientific rigour.

In these circumstances the National Museum of Victoria Council and the Victorian Institute of Marine Sciences Council were pleased to sponsor a workshop discussion by leading international cephalopod specialists in Melbourne (9-13 March, 1981). Discussions centred on two main themes:

(i) to define the state of our knowledge about both the organismic and environmental biology of cephalopods, and
(ii) to assess the potential for developing and utilizing cephalopods as a major marine resource.

This report provides a summary of the proceedings and the recommendations from the workshop as well as the majority of the contributed papers.

On behalf of both Councils I would like to thank the participants for giving their time and expertise to this important event. Special acknowledgement is due to Dr. C. C. Lu of the National Museum of Victoria, Mr. John Thompson formerly of the Victorian Institute of Marine Sciences and Dr. Clyde Roper of the Smithsonian Institution, Washington, for their efforts in organising and managing the workshop so effectively.

I would also like to thank the Australian Department of Primary Industry, the Australian Department of Science and Technology, the Victorian Ministry for Conservation, the Australia-Japan Foundation, the National Museum of Victoria Council, the Victorian Institute of Marine Sciences Council and the Australian Fishing Industry Research Trust Account for generous financial support. The Victorian Ministry for Conservation also made available the excellent facilities at the Marine Sciences Laboratories at Queenscliff as the venue for the workshop.

B. R. Wilson
Director, National Museum of Victoria

June, 1983

INTRODUCTION

In any consideration of marine communities, our understanding of major faunal groups, their significance, and interactions within trophic webs dwindles as we move away from the lower trophic levels. Similarly, our knowledge of macro-organisms, in both benthic and pelagic ecosystems, dwindles as we move away from animals of present day economic importance, e.g., fishes and mammals. Although important and impressive advances have been made in the past two decades, one of the most serious problems faced by marine and fishery biologists is an elucidation of the biology and ecology of top-level predators. A knowledge of their biology becomes imperative when we consider that world fisheries often are based on a harvest of such animals and, additionally, when we realize that many stocks presently being commercially exploited are in danger of serious depletion.

Interest in cephalopods has increased dramatically since 1945 because of (1) their sudden entrance into the world fisheries as a major human food resource, (2) their unique value in biomedical research, and (3) renewed studies in their biology and systematics. Apart from their importance in basic scientific research, the biomedical, behavioural and fisheries requirements showed a serious lack of knowledge of these animals in almost all aspects. Except for only two or three species of squid, very little is known about spawning and spawning grounds, duration of larval life, occurrence, life span, age at maturity, fecundity, growth rate, population size, migration, and role in the food web. Hence, the world-wide cephalopod fishery in 1945 produced about 500 000 tonnes, now produces about 1.0 to 2.0 million tonnes, and may have a possible annual production of 100 to 300 000 000 tonnes (Voss, 1973).[1] This world-wide fishery has an uncertain future unless the stocks can sustain an expanded fishery.

The role of cephalopods in the biological economy of the sea is even more complicated, for we have only fragmentary knowledge of the prey-predator relationship of cephalopods with other animals. Fields (1963)[2] suggested that fluctuations in anchovies in California are due directly or indirectly to cephalopod predation. In areas such as the Saharan Bank and Gulf of Thailand, overfishing of fin fish has resulted in their replacement by vast numbers of cephalopods; their total value now exceeds that of the fin fish they replaced (Voss, 1973).

Valid scientific and economic reasons exist for focusing on some of these problems. The international workshop on Problems of Assessing Populations of Nekton (Pearcy, 1975)[3] singled out the importance of cephalopods in pelagic communities (Clark, Okutani, Roper) and it is equally evident that populations of cephalopods in benthic communities are just as important to that system. In spite of increasing knowledge, too few data and syntheses are available to enable us to formulate predictive capabilities concerning these populations.

Knowledge of cephalopods has increased markedly in the past 20 years but many areas require critical attention. Not only is basic information needed on systematics, morphology, distributions and life cycles, but also the need exists to increase understanding of the complex ecological and trophic relationships of this group, with the ultimate goal of maximum development of the resource potential of many currently under-utilized species. Additional geographical areas also should be explored to designate species that can be exploited for academic and commercial purposes, that is, to increase basic scientific knowledge and to expand food resources.

The continuously increasing fishing pressure on cephalopods and their predators makes it imperative that we learn about the total biology of these forms while most populations still are relatively undisturbed. In an effort to achieve

[1] Voss, G. L., 1973. Cephalopod resource of the world. FAO Fisheries Circular no. 149: 1-75.

[2] Fields, W. G., 1963. Biology of *Loligo opalescens*. Proceed. xvi Intl. Cong. Zool. 1: p. 72.

[3] Pearcy, W. G. (Ed.), 1975. *Workshop on Problems of Assessing Populations of Nekton*. Off. Nav. Res. Rep. No. ACR 211: 30.

this and to foster a spirit of international understanding and cooperation, the Workshop on the Biology and Resource Potential of Cephalopods was conducted with the following objectives:

(i) to review, enumerate and discuss the state of knowledge about the organismic and environmental biology of cephalopods, including an assessment of the potential to develop and utilize cephalopods as a major marine resource for the future (e.g. food, biomedical research, etc.);
(ii) to identify the gaps in our knowledge about cephalopods;
(iii) to delineate subject areas that require research in the future, both at individual and co-operative levels, based on scientific and international importance as well as on the technological capability to do so;
(iv) to stimulate affiliations among cephalopod scientists in different fields.

A. SUMMARY OF THE WORKSHOP

1. Preface

The Workshop, jointly sponsored by the National Museum of Victoria and the Victorian Institute of Marine Sciences, was convened on 9 March 1981 at the Marine Science Laboratories, Queenscliff, Victoria, Australia. Mr J. Thompson of the Victorian Institute of Marine Sciences and Dr C. C. Lu of the National Museum of Victoria jointly planned and managed the Workshop. The participants included cephalopod researchers and fishery biologists from Australia and around the world.

The Workshop was organized into four major topic areas under which specific working papers were presented, each paper followed by extensive discussion. From the papers and discussions emerged a clearer picture of the current status of knowledge about each topic and a definition of the problems associated with these topics. Then a series of recommendations was developed in an effort to guide researchers, administrators, and officials in decision-making concerning future research and development associated with cephalopods.

The major topic areas were:

(i) Fisheries Biology and Assessment
(ii) Life History, Rearing and Aquaculture
(iii) Ecology and General Biology
(iv) Systematics and Morphology

The papers published in this volume are derived from the working papers presented in Queenscliff but most have been considerably refined and updated. Some papers were written as a result of the discussions and recommendations of the Workshop. Not all papers delivered during the Workshop are published here, because several presented preliminary work only and others have been published elsewhere.

2. Acknowledgements

The participants of the Workshop most heartily thank the National Museum of Victoria Council, and the Victorian Institute of Marine Sciences Council for their endorsement and support of the Workshop. We acknowledge and thank the Australian Department of Primary Industry, the Australian Department of Science and Technology, the Victorian Ministry for Conservation, the Australia-Japan Foundation, and the National Museum of Victoria Council for generous financial support for the Workshop. The Victorian Ministry for Conservation made available the excellent facilities at the Marine Science Laboratories at Queenscliff as the venue for the Workshop.

Grants toward the publication of the Proceedings were provided by the Australian Fishing Industry Research Trust Account, the National Museum of Victoria Council and the Victorian Institute of Marine Sciences Council.

Technical and secretarial assistance during the Workshop by Hilary Newton, Joan Phillips and Richard Tait, all of the National Museum of Victoria, is gratefully acknowledged. Technical and editorial assistance during preparation of the Proceedings was provided by Hilary Newton, Michael Sweeney, Laurie Marx and Sherry Petry.

Special thanks are due to John Thompson of the Victorian Institute of Marine Sciences for his assistance in organising and managing the Workshop, and to Dr B. R. Wilson, Director of the National Museum of Victoria for his support.

3. Program

MARCH 9 MONDAY	MARINE SCIENCE LABORATORIES, QUEENSCLIFF	
9.00 a.m.	Official opening of workshop by Professor J. Warren, President of the Council of the National Museum of Victoria	Prof. J. Warren
9.15 a.m.	*SYSTEMATICS AND MORPHOLOGY* Opening statements	*Group Leaders:* Dr C. Roper and Dr C. C. Lu
10.30 a.m.	Morning Tea	
10.45 a.m.	*Systematics and Morphology*—General Discussion	
12.00 noon	Lunch	
2.00 p.m.	*Systematics and Morphology*—General Discussion	
3.15 p.m.	Afternoon Tea	
3.30 p.m.	*ECOLOGY AND GENERAL BIOLOGY* Opening statements	*Group Leaders:* Dr T. Okutani and Ms V. Wadley
4.45 p.m.	DINNER BREAK	
8.00 p.m.	Informal discussion on current research programs and future research priorities in relation to *Systematics and Morphology.*	Discussion led by Dr C. Roper and Dr C. C. Lu
MARCH 10 TUESDAY	MARINE SCIENCE LABORATORIES, QUEENSCLIFF	
9.00 a.m.	Welcome from Dr R. Kelly, Director, Marine Science Laboratories	Dr R. Kelly
	ECOLOGY—General Discussion	Discussion led by Dr T. Okutani and Ms V. Wadley
10.30 a.m.	Morning Tea	
10.45 a.m.	*Ecology*—General Discussion	
12.00 noon	Lunch	
2.00 p.m.	*LIFE HISTORIES, REARING AND MARICULTURE* Opening statements	*Group Leaders:* Dr S. Boletzky and Dr R. Hanlon
3.15 p.m.	Afternoon Tea	
3.30 p.m.	*Life Histories, Rearing and Mariculture*—General Discussion	
4.15 p.m.	DINNER BREAK	
8.00 p.m.	Informal discussion on current research programs and future research priorities in relation to *Ecology, General Biology and Life Histories, Rearing and Mariculture.*	Discussion led by Dr S. Boletzky and Dr R. Hanlon
MARCH 11 WEDNESDAY	MARINE SCIENCE LABORATORIES, QUEENSCLIFF	
9.00 a.m.	*FISHERIES BIOLOGY AND ASSESSMENT* Opening statements	*Group Leader:* Dr G. Voss
10.30 a.m.	Morning Tea	
10.45 a.m.	*Fisheries Biology and Assessment* General Discussion	
12.00 noon	Lunch	
2.00 p.m.	*CASE STUDY—BASS STRAIT SQUID FISHERY*	Mr A. Harrison
3.15 p.m.	Afternoon Tea	
3.30 p.m.	Case Study—Bass Strait Squid Fishery (continued)	Discussion led by Mr A. Harrison and Dr G. Voss
4.45 p.m.	DINNER BREAK	
8.00 p.m.	Informal discussion on current research programs and future research priorities in relation to *Fisheries Biology and Assessment.*	Discussion led by Mr A. Harrison and Dr G. Voss
MARCH 12 THURSDAY	Field visits and activities	
	Group leaders draft reports and statements	
	All participants return to Melbourne	

MARCH 13 FRIDAY

9.00 a.m.	Consideration of draft reports and statements by group discussions
10.30 a.m.	Morning Tea
10.45 a.m.	Group discussions (continued)
12.00 noon	Lunch
2.00 p.m.	Plenary session Presentation of reports and recommendations
3.15 p.m.	Afternoon Tea
3.30 p.m.	Summary of workshop— Professor J. Swan, President, Victorian Institute of Marine Sciences
	General Discussion Closing remarks by Professor Swan
7.00 p.m.	Official dinner

MARCH 14 SATURDAY

9.00 a.m.	Group leaders finalise reports for initial editing.

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(Names followed by * were unable to attend the Workshop but contributed working papers.)

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B. SUMMARY OF RECOMMENDATIONS

The recommendations that resulted from the Workshop on Biology and Resource Potential of Cephalopods were presented as a report to the sponsoring agencies immediately following the workshop. While a number of recommendations appear in the texts of the various workshop papers, they are consolidated and summarized here as a unified presentation of the views of the workshop participants.

1. Preface

Cephalopods occur in all marine habitats of the world; they are extremely important in ecological, biological and biomedical research, and they represent an increasingly significant world-wide fisheries resource.

The Workshop on Cephalopod Biology and Resource Potential consisted of discussions carried out in plenary sessions, organized according to the subject areas of four working groups: systematics and morphology; ecology and general biology; life cycles and culture; and fisheries biology and assessment. Several issues were considered under more than one theme. For the sake of completeness, conclusions and recommendations are given here in the form presented independently by the four working groups. Recurrent statements bear witness to common problems and concerns in the various disciplines. For example, the question of the extent of fluctuations in population densities under natural conditions, i.e. independent of fisheries impacts, is considered under two different categories. As no comprehensive model of the life history strategies of cephalopods exists as yet, the statements made on the causes and significance of fluctuations in populations may not be identical. These apparent inconsistencies simply are a reflection of the poor state of our knowledge.

2. Systematics and Morphology

Lack of taxonomic knowledge is a major impediment to the progress of research on and utilization of cephalopods. The following recommendations are intended to alleviate these impediments in Australia and on a world-wide basis, and to assist the development of sound taxonomic knowledge of cephalopods.

a. *Priorities for Taxonomic Research*

(1) Four major families of commercially and ecologically important cephalopods are designated as requiring immediate and comprehensive systematic research on a world-wide basis:

Sepiidae –	the cuttlefish
Loliginidae –	the inshore squid

Ommastrephidae— the neretic and pelagic squid
Octopodidae— the inshore benthic octopus

(2) The speciose genus *Nototodarus* (Ommastrephidae) constitutes a major fishery resource in New Zealand and southern Australian waters, but the number of species and their distributions are unknown. A bi-national co-operative study on the taxonomy of this genus could eliminate the taxonomic impediment which presently inhibits research and development of this valuable resource.
(3) At a second level of urgency taxonomic research should be encouraged on the entire cephalopod fauna as opportunities, interest and requirements arise.

b. *Collections*
(1) Insufficient collections of cephalopod specimens exist in most museums and laboratories of the world. An effort must be made to accumulate systematic collections of all life stages to serve as a basis for taxonomic and morphological research on local, regional, and global scales.
(2) Scientists and research organizations should recognize the importance of voucher specimens (preserved samples of the populations upon which research has been conducted) and deposit such samples in appropriate museums for safe-keeping and future reference.
(3) Selected cephalopod specimens derived from fisheries and environmental surveys and research programs conducted by State and Federal fisheries and environmental agencies should be lodged in appropriate State museums, as a contribution to the development of taxonomic research on these animals.
(4) Scientists and research organizations depositing material in museums must ensure that accurate and complete sets of data (e.g. station data, collecting information) accompany the specimens.
(5) Organizations and grant-supported researchers who deposit significant cephalopod reference collections in museums should recognize the resultant stress placed on museum resources and budget to cover the initial curatorial costs (e.g., preservatives, glassware, cataloging and data entry, labelling). Consultation with museum curators on preservation techniques and data requirements should precede the budget planning and field programs.
(6) Museums holding cephalopod material should encourage taxonomic research by making it freely available to research workers, according to their institutional policies. Researchers should accept the principle of depositing primary type material in an appropriate museum in the country of origin.

c. *Publications*
(1) Manuals. Specific documents resulting from this working group should be published to stimulate and facilitate systematic research on cephalopods:
  (a) Manual of Techniques for Preservation of Cephalopods
  (b) Guidelines to Minimum Standards for Description of Cephalopod Species.
(2) Reviews: The working group recommends the establishment of an international team of systematic specialists to produce and publish "Reviews of Cephalopod Taxa" as a series, similar in style and purpose to the FAO Identification Sheets series.

These publications will review the current status of taxonomic knowledge within particular families or genera, describe and provide keys to the known taxa, and provide

bibliographies and lists of current research workers in specific taxa.

Preliminary manuscripts will be solicited by a team from the present workshop participants during the next three years, and will be tested and completed at a future workshop.

d. *Permanent Working Group*

The current working group recommends the establishment of an international body of experts on cephalopod biology with the following functions:

(1) to provide information about cephalopods to research and fisheries agencies;
(2) to co-ordinate international workshops and meetings;
(3) to make recommendations concerning cephalopod research;
(4) to set up training courses on the identification and study of cephalopods.

Note: The first meeting of the Cephalopod International Advisory Committee was convened in Plymouth England in June, 1981. Nine charter members, including a chairman were appointed to stand for two years. The next workshop/meeting will be held in 1983. For additional information contact Malcolm Clarke, Executive Secretary.

3. **Ecology and General Biology**

Because of substantial gaps in knowledge about cephalopods, especially those of economic importance, often it is not possible to provide basic biological information required for fishery assessment and management.

a. *Predator and Prey Relationships*

Cephalopods are key components in the trophic framework of marine communities, comprising an essential part of the diet of many fish, marine birds, mammals, and other cephalopods. In turn, cephalopods feed extensively on fishes, crustaceans and other cephalopods. The presence of cephalopods thus exerts a major influence on the structure of marine ecosystems and on populations of marine animals, including commercially important species. Feeding habits of cephalopods change with sequential growth stages. Specific feeding habits and dietary composition may provide supplementary information on the systematics and population structure of cephalopods. Parasites and chemical elements are useful as tags and tracers for elucidating trophic interactions. These tags and techniques such as the electrophoretic analysis of proteins have application in defining populations or subpopulations.

b. *Life Cycles and the Environment*

In general cephalopods are short-lived, fast-growing and highly fecund. They undergo natural fluctuations in abundance and probably repopulate easily following reductions in numbers. These factors apparently allow them to survive largely independent of environmental conditions and fishery pressures (at least of the kind demonstrated to alter the abundance of some marine mammals and elasmobranch fish). Fishery and mariculture biologists, however, need to know exactly what roles are played in this strategy for survival by spawning, hatching, growth, life-span and mortality on the one hand, and by the biotic and abiotic factors of the environment, on the other hand.

c. *Public Health*

Ecological research embraces the potential problem of public health associated with parasites and toxic heavy metals which may be concentrated in the flesh of cephalopods ingested by humans. The following recommendations pertain to some of the key difficulties:

(1) Taxa to which ecological research should be directed. Priority should be given to those cephalopods of established or potential economic importance, particularly the:

Sepiidae
Loliginidae
Ommastrephidae
Octopodidae

(2) Trophic Position. Cephalopods are key organisms in the trophic framework of marine communities as both prey and predator. It is recommended that a high priority be given

to classification of the trophic position of target species and the effects of fluctuations in cephalopod populations on stocks of other species (e.g. fish, birds, marine mammals) that are prey or predators of cephalopods.

(3) Feeding Habits and Nutrition. It is recommended that research be focused on the diet of target species of cephalopods, including nutrient requirements, conversion efficiency and rate of the digestive process and that such studies consider all the life stages of the species.

(4) Reproduction. We recommend research on the reproduction of target species, especially on the identification of spawning seasons and sites, translocation of larvae, schooling and migration behaviour, and the influence of environmental factors on these functions.

(5) Parasites. Research is recommended on the identification of the parasites of cephalopods that may be harmful to fishery stocks or capable of transmission to humans, thus constituting a potential public health hazard.

(6) Heavy Metals. We recommend research on the concentration of toxic heavy metals in the flesh of cephalopods which may be ingested by humans, with consequent health problems.

(7) Population Biology. Urgency should be given to research aimed at determining the major factors that influence the size and structure of cephalopod populations and subpopulations by studying both biotic and abiotic aspects of the environment. However, before long-term monitoring is planned, the objectives should be carefully formulated to answer specific questions about cephalopod populations. Such studies would involve long-term ecological monitoring in conjunction with fisheries biology and physical and chemical oceanography.

4. **Life Cycles and Culture**

Understanding life cycles is essential for the proper utilization of species that are important to research and commerce. Culture may be thought of as the tool with which critical aspects of life cycles may be worked out by rearing cephalopods through part or all of their life span under controlled conditions. Past experience has clearly shown that complementary field and laboratory studies must be carried out to produce an overall understanding of the entire cycle.

Of particular need is information on feeding, growth, behaviour, and reproduction (i.e., sexual maturation, fecundity and spawning, etc.) in order to (a) understand the life cycles of commercially exploited species, and (b) rear appropriate species under controlled conditions to provide a source of live research material for a wide range of basic scientific investigations (e.g., physiology of organ systems, cell membrane permeability, nerve propagation, etc.).

Neither market demand nor culture methodology is sufficient to warrant the culture of cephalopods for human consumption at this time. But the demand is high for cephalopods as experimental models for basic research and the methodology for culturing many of them on a small scale is sufficiently worked out that this approach should be used to solve specific problems related to an animal's life cycle in nature.

The following recommendations are considered to be achievable and worthy of priority attention:

a. *Life Cycle Study in the Laboratory*

Laboratory studies should always be conducted in conjunction with field studies to help elucidate specific aspects of life cycles. The laboratory studies should concentrate on *early* life history, particularly on feeding, growth and behaviour. Factors that influence fecundity, onset of sexual maturation and spawning should be studied in laboratory conditions.

b. *Longevity*

Priority should be given to development of techniques to determine the age of individuals using periodic growth

structures (such as statoliths, cuttlebones, etc.) because of the importance of age determination in stock assessment. Such techniques are most accurate if the quality and number of growth rings or chambers, as related to age, are known from laboratory-reared animals of known age.

c. Artificial Food

Development of an artificial food ration for cephalopods to replace the high-priced food currently used in culture work is an urgent need in support of culture work. Growth characteristics under artificial feeding conditions must be tested by using periodic growth structures, possibly statoliths, as a reference.

d. *Species Selected for Study*

At present the life cycles of only a few "standard" species of cephalopods have been studied in laboratory conditions. Along with the refinement of cultural and analytical methods applied to them, exploratory studies on new and little-known cephalopods must continue, as any species may have the potential for research and exploitation in medical, fisheries and other fields. So little is known of this field that it is not possible at this stage to select taxa worthy of priority attention.

5. **Australian Squid Fisheries Biology and Assessment**

At the early stages of fisheries development a need exists for interim management measures ensuring that "safe" harvesting levels are respected. This must not preclude any further development. The key issue is *how much squid can be taken* without disturbing the balanced ecosystem to which these animals belong. Therefore we must concentrate on the quantification of natural excess production that can be tapped by fisheries.

The population dynamics of cephalopods are characterized by the effects of a short life span, rapid growth, high fecundity, and migration patterns that may or may not be directly related to uneven distribution. Thus stock abundance is likely to be affected greatly by environmental factors and hence to fluctuate widely. Models must allow for these factors.

In assessing squid stocks many difficulties arise from a pervading lack of information on the biology of the species involved (see previous sections). Throughout the world most data are derived from jig fishing. Only data from this source are presently available for the Australian fishery. This technique catches animals only within a limited size range and during a limited season.

The squid fishery of Australia is a recent development. So far it has been dominated by foreign interests, being conducted to a large extent by foreign vessels. As there is little historical information on squid resources, Australian fisheries agencies rely on catch statistics derived from these vessels and from the cooperative research program carried out with the Japanese vessel *Hoya Maru*.

Further development of the Bass Strait fishery is called into question by fears of local fishermen and fisheries authorities concerning possible food-web alterations by a large squid fishery, adversely affecting traditional fin fish populations by reduction in food. The situation requires immediate attention as it relates to licensing quotas for foreign squid vessels. Should numbers be maintained or increased, or should they be decreased in response to the fishermen's reservations?

This matter was discussed at length by the squid biologists at the Workshop. There are no data available which bear on this problem, and no indirect subjective evidence. However, the consensus of opinion, based on knowledge of squid biology and squid fisheries elsewhere, was that fluctuations of squid populations are unlikely to affect the fin fish population.

Also, from the data available from the Bass Strait squid fishery the Working Group saw no danger to the squid stocks at the current level of vessel involvement. So far these stocks have not been heavily exploited and present fishing efforts will not deplete them.

The Working Group makes the following recommendations based on the participants' collective experience and consideration of the data presented to the Workshop:

a. *Short Range Program*

(1) The number of vessels licensed for the Australian squid fishery, and catch

quotas, should not be reduced in the near future.

(2) The quality and quantity of data collected from fishing vessels should be improved and increased, concentrating on catch composition, maturity stages and size frequencies. Specialized observers and trained crew members should be involved in data collecting.

(3) A limited number of Australian and foreign vessels equipped with squid jigging gear should be encouraged, and possibly subsidized in the initial stage, to carry on fishing and data collection in southern Australian waters during the winter months, as data for that season are entirely lacking. A winter squid fishery could occupy fishermen who are engaged in other fisheries during the summer.

(4) A research vessel equipped for offshore work with jigs, otter trawls, gill nets, midwater trawls and plankton nets should be devoted to a regular squid fishery resource survey in Australian waters.

(5) Cooperation with the proposed Tasmanian hydroacoustic program should be established for a detailed survey of bottom configurations in Bass Strait, and for plankton and squid assessment with the acoustic integrator system.

(6) The statistical program on squid catches (including the Taiwanese loliginid fishery in northern Australia) should be unified between Australia and New Zealand.

b. *Long Range Program*

Collections of specimens and data over several years will be necessary to define the biological basis for a viable long-range fishery.

(1) Ecological data on the sea bottom complementary to known characteristics of hard and soft substrates should be collected in the continental shelf and slope areas, especially in order to locate and protect spawning areas.

(2) A periodic survey program should be established, with a series of stations, covering the area from north of Sydney, around Tasmania, and into the middle part of the Great Australian Bight. Complementary samples from Perth and Brisbane areas should be used in defining populations and species. Sampling gear should include jiggers, otter trawl, gill net, plankton net and dip net with night lighting.

(3) Efforts should be made so that New South Wales, Victorian and South Australian fisheries agencies cooperate in the echosounding survey currently proposed by the Australian Maritime College in Tasmania.

(4) A system of catch discrimination for fishermen should be developed using simple, visual charts to identify species.

(5) Specimens obtained at remote stations of the study area should be analysed for morphometric and electrophoretic discrimination of possible population or sub-specific differences. The use of parasite tags may help in defining populations.

(6) Areas around stations that have provided mature stage VI females should immediately be sampled to determine areal and temporal limits of spawning. Fecundity should be determined, taking into account the possibility of prolonged spawning and the corresponding delay in maturation of part of the ovarian eggs.

(7) Stratified series of horizontal plankton tows should be made at each station from the surface to the bottom to determine the depth distribution of the hatchlings and eggs. Additional sampling of early cephalopod life stages should be carried out from "ships of opportunity" such as ferry boats and passenger vessels, using "high-speed" plankton samplers. Regional universities could cooperate in sorting and analysis.

(8) Specimens obtained in fisheries studies should be deposited in museums as voucher material and to support future research. Information on holdings should be exchanged between museums and laboratories. (See also Recommendation 2 of the Working Group on Systematics and Morphology.)

(9) Museums should be supported through state and federal fisheries agencies to curate and maintain their collections; trained assistants are most critically needed. The maintenance of collections is a specific museum function that requires special techniques and facilities not normally available in fisheries and marine laboratories.

(10) Australian cephalopods, in addition to *Nototodarus*, should be investigated to determine their potential for fisheries development. Biological data should be accumulated so Australia will be prepared to assess stocks when new fisheries develop.

(11) Since generalizations about squid behaviour are not advisable, laboratory or field observations of behaviour of local squid in relation to fishing should be undertaken to improve or modify existing squid jigging or gill netting techniques.

(12) The following factors should be considered in conducting squid-jigging or gill net fisheries:

(a) light attraction—research on efficient lamps in terms of maximum attraction and economy;

(b) squid jig—"Oppai-bari" (transparent stem jigs) interspersed with standard jigs produce better catches according to catch data from Japan;

(c) squid lines—for daily squid jigging operations, jig lines (nylon monofilament) should be changed after ten days of continuous use;

(d) quality of catch—squid gill net fishing is about three times more efficient than jigging, but the quality of the catch is lower because of damage to the body.

AN OVERVIEW OF CEPHALOPOD SYSTEMATICS: STATUS, PROBLEMS AND RECOMMENDATIONS

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Abstract

This paper reviews the current status of systematics of Recent cephalopods (squids, cuttlefishes, octopuses and nautiluses) on a world-wide basis. It includes lists of recent revisionary publications (1960-1981), and revisions in progress. Problems that impede progress in cephalopod systematics are discussed, including the taxonomic and geographic complexity of the group, lack of comprehensive collections and well preserved specimens, scarcity of classical studies, scattered literature, and lack of funding for research and education. The situation in Australia is cited as an example of the status of cephalopod systematics in most other regions of the world. A list of Australian species in four major families (Sepiidae, Loliginidae, Ommastrephidae, Octopodidae) is presented, as is a bibliography of the cephalopod biological literature of the Australian region.

Recommendations are given in an effort to improve the status of cephalopod systematics and consequently to provide information required in other fields (e.g., biomedical research, behavior, ecology, parasitology, fisheries biology): (1) recognition of need for research and education and for increased funding to support them; (2) training and development of regional (geographic) specialists as well as taxon-oriented (world-wide) specialists; (3) support and production of keys to identification, catalogues of important collections, and revisions and monographs; (4) establishment of national, regional, and world-wide authoritative reference collections; (5) designations of four major families of cephalopods in critical need of comprehensive systematic revision (Sepiidae, Loliginidae, Ommastrephidae, Octopodidae).

Introduction

Voss (1977) presented an historical account of major systematic works and pointed out reasons for the comparatively primitive state of our knowledge concerning cephalopod systematics. The present review deals with the broader aspects of systematics and morphology in the context of the theme of the International Workshop on the Biology and Resource Potential of Cephalopods (Melbourne, Australia, March, 1981). The topics discussed include the current status of systematics in cephalopods, problems that impede the progress of cephalopod systematics, the status of systematics of Australian cephalopods, and recommendations for enhancing systematic programs in cephalopods that will aid fisheries scientists as well as advance general systematic knowledge.

The term "systematics" (taxonomy) is used here in its broadest sense to cover all aspects from descriptions of taxa, classification, phylogeny, zoogeography, taxonomic life history, population analysis, and comparative and functional morphology. The basis of all modern systematics, of course, is morphology.

Ideally, a thorough knowledge of the systematics of a species is the required foundation upon which all other biological and resource management studies must be based, because the biology of each species is different. This ideal, however, is seldom realized for a variety of reasons. Comprehensive collections, time, and trained specialists, to mention only a few, are the necessary requirements for thorough systematic studies.

Several examples of the lack of systematic knowledge about cephalopods exist in reference to fisheries. Several years ago a vigorous fishery developed for squid in New Zealand waters, based on the single known species in the area, *Nototodarus sloani* (Gray, 1849), which is restricted to those waters. As biological information accumulated for support of the fishery and for development of a management scheme, significant inconsistencies in occurrence and distribution became apparent. Requested systematic studies then confirmed the presence of a second species, *Todarodes filippovae* Adam, 1975, which subsequently has been recorded circum-globally in the southern regions of all three oceans. More recently, detailed biological studies have demonstrated the existence of several distinct populations of the two known species, as well as the presence

of a third, undescribed species (Smith, Roberts & Hurst, 1981).

In the Gulf of Campeche, Mexico, a traditional fishery was based on *Octopus vulgaris* Lamarck, 1798, a ubiquitous octopus of broad distribution. In the absence of local studies, knowledge about the biology of *O. vulgaris* from other seas was applied to the Campeche octopus for fishery statistics and management purposes. The discovery that the octopus was indeed a new species, described as *O. maya* Voss and Solis, 1966, with a very different life history, explained the problems that had plagued biologists assigned to study the fishery and develop recommendations.

More recently, an expanding fishery has developed in Australia based on the ommastrephid squid, *Nototodarus gouldi* (McCoy, 1888). Australian fisheries agencies are interested in accumulating sufficient knowledge in order to formulate management plans before the population becomes too severely impacted by the fishery, a most commendable goal. However, the recent discovery of another species of *Nototodarus* sympatric in the northern range of *N. gouldi*, as well as *Todaropsis eblanae* (C. C. Lu, pers comm., 1982), dictates a very cautious and detailed approach. The existence of seven additional species of ommastrephid squids (M. Dunning and C. C. Lu, pers. comm.) now known to inhabit Australian waters graphically demonstrates the need for immediate, intensive systematic studies.

These examples vividly demonstrate that we must have sound systematic knowledge about species and populations if we are to approach the truth about the biology, ecology, behavior, and fisheries of these forms. But frequently scientists in these disciplines cannot wait for systematic revisions to be completed. Often, the best that can be hoped for is an identification of the species being studied or fished based on the most recent revision, which may, in fact, be decades old and not comprehensive in geographical coverage, life stages, etc. Clearly this does not solve the problems.

Current Status

General Review.—The status of cephalopod systematics perhaps can be reviewed best by listing the revisions published during the last two decades, the "recent era" (Table 1). I have interpreted the term revision rather broadly, so that researchers interested in a particular group will have a starting point; therefore, several works listed are not true revisions in the strict systematic sense. Further, it is interesting that most of the works deal with families and genera with (1) small numbers of species, (2) oceanic or deep-sea forms, or (3) small-sized animals. While some of these studies may be very important to cephalopod systematics and phylogeny in general, they are of little help to fisheries biologists or others who need systematically

TABLE 1

Systematic Revisions of Cephalopoda, 1960-1981.*

Adam and Rees (1966)—Sepiidae
Adam (1979)—Australian Sepiidae
Clarke (1980)—beaks from predators
Cohen (1976)—western Atlantic *Loligo*
Hochberg (1980)—Gulf of California Octopods
Imber (1978)—southern Pacific Gonatidae & Cranchiidae
Kristensen (1981)—Atlantic *Gonatus*
Kubodera and Okutani (1977 & 1981)—Pacific *Gonatus*
Kubodera and Okutani (1981)—Pacific teuthoid larvae
Mangold-Wirz (1963)—Mediterranean Cephalopoda
McSweeney (1978)—*Galiteuthis*
Natsukari (1975—with Okutani & 1976)—Pacific loliginids
Nesis (1972 & 1974)—Cranchiidae
Nesis (1973)—Gonatidae
Okiyama (1969 & 1970)—*Gonatopsis*
Okutani (1973 & 1974)—Western Pacific squids
Okutani (1976—with Satake, Ohsumi, & Kawakami, & 1978—with Satake)—Sperm whale diet
Okutani (1981)—Indian Ocean *Onykia*
Roeleveld (1972)—South African Sepiidae
Roper (1969)—Bathyteuthidae
Roper, Lu, and Mangold (1969)—*Illex*
Roper and Young (1968)—Promachoteuthidae
Roper, Young and Voss (1969)—Key to teuthoid families
Saunders (1981)—*Nautilus*
Taki (1961, 1963, 1964)—Octopodidae
Thomas (1977)—Tremoctopus
Voss, G. (1962)—Lycoteuthidae
Voss, G. (1963)—Philippine Cephalopoda
Voss, G. (1968 & 1971)—Octopodidae
Voss, G. (1976)—Deep Water Octopoda
Voss, N. (1969)—Histioteuthidae
Voss, N. (1974 & 1980)—Cranchiidae
Wormuth (1976)—Pacific Ommastrephidae
Young (1972)—Eastern Pacific Cephalopoda
Young and Roper (1968)—Batoteuthidae
Young and Roper (1969)—Cycloteuthidae
Young and Roper (1969)—Joubiniteuthidae

* Full citations are included in the Literature Cited section.

sound information. Curiously, the families most in need of comprehensive, systematic revisions are those that are of greatest importance to fisheries on a world-wide basis. These include:

- Sepiidae, the cuttlefishes; *Sepia*, *Sepiella*
- Loliginidae, the inshore, neritic, myopsid squids; *Loligo*, *Doryteuthis*, *Lolliguncula*, *Loliolus*, *Sepioteuthis*, *Alloteuthis*, *Uroteuthis*, *Loliopsis*
- Ommastrephidae, the neritic and upper pelagic oceanic squids; *Illex*, *Todarodes*, *Todaropsis*, *Nototodarus*, *Ommastrephes*, *Dosidicus*, *Ornithoteuthis*, *Symplectoteuthis*, *Martialia*
- Octopodidae, the inshore, benthic octopuses; *Octopus*, *Cistopus*, *Hapalochlaena* etc.

Species of these four families sustain approximately 90% of the world's fisheries catch. (Species of the Gonatidae and Onychoteuthidae are emerging as exploited stocks but their contribution to the total catch currently is small; certainly they require systematic treatment as well.)

Table 2 lists the groups (families or genera) of cephalopods known to be under revision currently. Here again most of these revisions are on groups that have little direct application to fisheries, with the exception of the ommastrephids, loliginids, and possibly the gonatids and octopods. There is, of course, important indirect application of these revisions as well as those already published, in that most of these cephalopods form an extremely significant part in the diets of many fishes and toothed whales of commercial importance. Other marine mammals and pelagic birds prey extensively on cephalopods as well, so systematic knowledge of all groups indeed is valuable to biologists studying other marine organisms.

TABLE 2

Revisions of Cephalopod Groups Known to be in Progress.*

Burgess—Central Pacific *Abralia* and *Abraliopsis*; *Enoploteuthis* (1982)
Bublitz—North Pacific Gonatidae
Clarke—Keys to cephalopod beaks
Hochberg—Eastern Pacific octopods
Kubodera and Kristensen—Gonatidae
Lu—Australian Loliginidae and Ommastrephidae
Roeleveld—Ommastrephidae
Roper and Young—Chiroteuthidae
Roper and Sweeney—Brachioteuthidae
Toll—Octopodidae
Voss, G.—Enoploteuthinae, *Abralia* and *Abraliopsis*
Voss, G.—Cirrata, deep-sea octopods
Voss, N.—Cranchiidae

* Please consult with individual authors concerning the status of these revisions; addresses are provided in Appendix 1.

Problems.—The large families, so important as fisheries resources, largely have been ignored insofar as their systematics are concerned. Their importance is universally recognized, not only in fisheries but in prey-predator, behavioral and biomedical research, and yet they seem to remain untouched. Why? Some of the reasons are linked to the problems that we face in systematics in general and these are compounded by a few specific problems, such as large numbers of poorly known species. The four major families mentioned above comprise about 50% of the known species of cephalopods. Estimates indicate that there are over 100 species of octopodids, about 100 species of sepiids, 40 to 50 species of ommastrephids, and 60 to 80 species of loliginids; so the largest, most speciose families of cephalopods must be dealt with. As most of the genera at least are world-wide in distribution, systematic collections are grossly inadequate. Also the literature is widely scattered, in many different languages and journals, and of widely varying quality. Furthermore, often it is difficult to get the literature, particularly the older, obscure, but nonetheless important works. Another reason is that the type specimens, the specimens upon which species names are based and which are so vital for comparative studies, no longer exist in many cases and no lectotypes have been established. Because of the soft-bodied nature of cephalopods, they require special attention for initial fixation and long-term preservation. Many older specimens lacked that attention, and were allowed to dry out or are in such poor condition that the important systematic characters are no longer distinguishable. It is very discouraging for a systematist to visit an old museum with great anticipation which

quickly dissolves to disappointment when the holotype turns out to be a bit of sludge or slurry in the bottom of the jar. Poor fixation and preservation are not limited by any means to the old collections. While it is not universally true, very frequently if a systematist wants to have good systematic-quality specimens, properly fixed and preserved material, he must collect and prepare them himself, or at least instruct others on proper techniques of fixation. (Guidelines to techniques of preservation are published elsewhere in these proceedings (Roper & Sweeney, 1983)).

Samples taken during fisheries surveys or non-systematically oriented collecting programs frequently are most conveniently frozen. Thawed specimens or those casually fixed after freezing, however, do not make adequate material for systematic analysis. For example, many characters, such as the viscera and the hectocotylus, become soft, flacid, and amorphic; sucker rings, often of such great taxonomic value, become dislodged from the suckers and lost. Fixation of at least a portion of the fresh sample in 8-10% buffered formalin will ensure that important taxonomic characters are preserved; fixed material should contain both males and females as well as specimens from the whole range of sizes available.

Octopuses fixed in formalin (or other fixative) while still alive are extremely difficult if not impossible to work with, because they contract so vigorously that their arms become tightly coiled, immeasurable coil springs, the mantle a solid lump, and the viscera, a congealed, half-rotted mass, untouched by fixative that could not penetrate rapidly enough through the contracted mantle muscle and closed-off mantle opening. To avoid these problems, octopuses must be narcotized or killed in fresh water, then fixed while the arms are kept straight. No cephalopod, squid, cuttlefish or octopus, should ever be fixed in a container shorter than the total length (less tentacles of squids and cuttlefishes) of the specimen. The soft-bodied creatures become permanently molded in the position they initially are fixed in, whether they be squeezed into a jar or laid out in a tray. (Of course, if no selection of containers exists, a specimen may be carefully folded at the neck and fixed, rather than have no specimen.)

Another hindrance to major systematic studies on cephalopods is the problem of adequate samples. Too frequently the collections are poorly preserved, from widely scattered localities, inadequate in numbers, and lack various life stages. The life stages of very few species are known. In fact, in many of the oceanic species only the larvae and juveniles have been described. Moreover, specimens of large species, e.g., of *Architeuthis*, *Moroteuthis*, ommastrephids often are not preserved. Only in the last decade or so with the use of very large mid-water trawls and examination of predator gut contents have we begun to acquire adults of many forms (Clarke, 1977, 1980; Roper, 1977). Cephalopods frequently are extremely difficult to catch; because they are very perceptive, and very fast swimmers, they are able to avoid the nets. Capturing adequate samples is so difficult, in fact, that those of us who sample oceanic and midwater groups insist that we catch only the slow, the sick and the stupid. A recent workshop on problems of assessing populations of macronekton addressed this problem (Wormuth and Roper, 1983). With cephalopods recognized as a extremely frustrating group for biologists, how can we begin to assess populations when we catch only two or three specimens? Adequate samples for purposes of identification and systematic study should consist of specimens of both sexes from the full range of sizes available and from as broad a geographic range as possible.

Still another problem in the systematics of cephalopods is related to the nature of their structure and morphology. Because cephalopods are soft-bodied, lack an external shell (except *Nautilus*), have no fin rays, no bones, and no spines, an element of frustration and difficulty is introduced. That is not to say that no taxonomic characters exist, but it does mean that systematics must search extremely diligently for taxonomic characters, some of which may be obscure and/or minute. Cephalopods, in general, don't have the type of meristic characters that occur in crustaceans, fishes and

shelled mollusks, for example. Furthermore, we still are at a very primitive stage in knowledge about the characters themselves. Until very recently, there seemed to be a lack of recognition and definition of new characters or character states. As yet, we don't know the range of variability of characters across the geographical range of most species, and we don't know how this range of variation applies to species, sub-species and populations. In part, this lack of knowledge is a result of the lack of adequate collections.

A further problem is that in general there is a lack of comparative systematic studies. Currently no internationally established standards exist for descriptions of cephalopods, so a wide variety in the quality of descriptions exists. The strong recommendation for the establishment of minimum standards for descriptions of cephalopod species was made during this workshop and has resulted in its implementation and publication in these proceedings (Roper & Voss, 1983). Each description of every new species of cephalopod published hereafter should follow these guidelines, so that all necessary characters are described. The botanists have very standardized techniques for describing species, as do many entomologists and crustacean taxonomists. Oftentimes authors describe only a few of the characters, only the most obvious ones, or only the positive characters, so that when more than the original specimen are examined, they are unidentifiable. We have claimed that no problem exists in the systematics of cephalopods as long as only one specimen is present, but as soon as a second is at hand, problems arise, because variation rears its Hydra-head and we simply do not know enough about variation in cephalopod characters and character states. We must increase our knowledge of all of the characters in cephalopods, positive and negative, so that we can conduct the detailed comparisons with other closely related species so necessary for a more thorough understanding of their biology.

Illustrations play a vital role in the descriptions of cephalopods, but currently as broad a range of variation exists in the quality of illustrations as in descriptions. Illustrations often are poorly rendered, lack detail, are absent altogether, or they appear as photographs. While a photograph may be adequate for the general habitus of a cephalopod, it is extremely difficult to show the fine details of characters of squids and other cephalopods (photomicrographs and SEM photos excepted). Lists of illustrations accompany the standards for descriptions mentioned above. Certain characters always should be illustrated and those required illustrations should be of a high standard. Standards of descriptions and illustrations will help form the basis for modern comparative morphological studies that lead to an understanding of the systematics and phylogeny of the group.

An attitudinal problem also exists. Because systematics often is looked upon as an archaic, unexciting science, it is difficult to attract students, researchers and science administrators to an appreciation of the necessity for systematic research. Part of the problem lies with systematists themselves who often have failed to promote their science. When personal attitudes and the archaic image are changed, systematics will attract more students and the field will advance. In fact, the field now seems to be enjoying a resurgence of "popularity" due largely to the application of new technology (e.g., scanning and transmission electron microscopy) and "new" analytical approaches, such as cladistics. Application of these techniques should be boldly encouraged and tested as tools to aid modern systematic research.

The lack of funding for systematic research is the last problem I shall discuss. Part of this problem is related to the attitudinal problem—systematics is not particularly trendy or flashy and that affects the thinking of funding agencies and administrators. Modern systematists require more support than the magnifying lenses and green eye shades of their predecessors of past centuries. As much money is required to support comprehensive, modern systematic research as for many other kinds of research. For example, if collections of marine organisms must be made, the cost of ship time alone can be very significant. Until additional funding is directed toward systematic research on cephalopods, the field will advance too slowly and too sporadically to meet the

demands for systematic information (identifications, fishery management, relationships, zoogeographic distributions, etc.).

Regional Example: Australia. — A bit of history concerning the systematics of cephalopods in Australia will serve as an example of the status of systematics in general. Perhaps Australian cephalopod history goes back to the days of Captain Cook. Certainly Captain Cook was greeted by stranded cuttlebones, as well as goannas (lizards) when he landed on Lizard Island in search of an escape route through the Great Barrier Reef. The Dutch and French were among the first to have made collections during their early exploring expeditions; the *Astrolabe* and the *Geographie*, for example, collected species that were described by Quoy and Gaimard in 1832. Gray described several Australian species in 1849 from material brought back by the British explorers. The major contributor to Australian cephalopod systematics in the 19th Century was W. E. Hoyle who in 1875 described the material from the *Challenger* Expedition that went up through the Coral Sea and the Arafura Sea. But, in general, the status of systematics of cephalopods in Australia largely has remained at a primitive level, primarily because no specialist in cephalopods has worked in Australia. T. Iredale did describe a large number of species and genera of cuttlefish based on cuttlebones, but all those taxa must be questioned until verified with specimens. (See Appendix 2 for a bibliography of Australian cephalopod literature).

The Australian state museums have collected cephalopod material and maintain collections. Reports of their holdings are included as papers in this volume (Lu, 1983; Rudman, 1983; Slack-Smith, 1983; Zeidler, 1983). Just as the four major families, Sepiidae, Loliginidae, Ommastrephidae and Octopodidae are considered in critical need of systematic revision on a world-wide basis, they are equally in need of revisionary studies in Australia. In Australia, members of these families are the most accessible, the most abundant, and the most important for active and potential fisheries. The species in these families are listed in Table 3 as an indication of their importance in Australian waters. These are species recorded or described from Australia but the validity of many must be verified by further investigation.

TABLE 3

Nominal species of Sepiidae, Loliginidae, Ommastrephidae and Octopodidae described or reported from Australian waters.

A. Sepiidae
- *Sepia*
  - *apama* Gray, 1849
  - *bandensis* Adam, 1938
  - *bartletti* (Iredale, 1954)
  - *baxteri* (Iredale, 1940)
  - *braggi* Verco, 1907
  - *chirotrema* Berry, 1918
  - *cottesloensis* (Cotton, 1929)
  - *cottoni* Adam, 1979
  - *cultrata* Hoyle, 1885
  - *dannevigi* Berry, 1918
  - *elliptica* Hoyle, 1885
  - *galei* Meyer, 1909
  - *gemellus* (Iredale, 1926)
  - *genista* (Iredale, 1954)
  - *glauerti* (Cotton, 1929)
  - *hedleyi* Berry, 1918
  - *hendryae* (Cotton, 1929)
  - *irvingi* Meyer, 1909
  - *jaenschi* (Cotton, 1931)
  - *lana* (Iredale, 1954)
  - *liliana* (Iredale, 1926)
  - *limata* (Iredale, 1926)
  - *macilenta* (Iredale, 1926)
  - *mestus* Gray, 1849
  - *mira* (Cotton, 1932)
  - *novaehollandiae* Hoyle, 1909
  - *occidua* (Cotton, 1929)
  - *opipara* (Iredale, 1926)
  - *ostanes* (Iredale, 1954)
  - *pageora* (Iredale, 1954)
  - *papuensis* Hoyle, 1885
  - *parysatis* (Iredale, 1954)
  - *pfefferi* Hoyle, 1885
  - *pharaonis* Ehrenberg, 1831
  - *plangon* Gray, 1849
  - *reesi* Adam, 1979
  - *rex* (Iredale, 1926)
  - *rhoda* (Iredale, 1954)
  - *rozella* (Iredale, 1926)
  - *smithi* Hoyle, 1885
  - *submestus* (Iredale, 1926)
  - *treba* (Iredale, 1954)
  - *vercoi* Adam, 1979
  - *versuta* (Iredale, 1926)
  - *whitleyana* (Iredale, 1926)

B. Loliginidae
- *Loligo*
  - *chinensis* Gray, 1849
  - *etheridgei* Berry, 1918
  - *edulis* Hoyle, 1885
- *Doryteuthis*
  - *sibogae* Adam, 1954
  - *singhalensis* (Ortman, 1891)

TABLE 3 continued

Loliolus
n. sp. Lu, Roper & Tait, In press
Sepioteuthis
australis Quoy and Gaimard, 1832
bilineata (Quoy and Gaimard, 1832)
lessoniana Lesson, 1830
C. Ommastrephidae
Nototodarus
Gouldi (McCoy, 1888)
sloani (Gray, 1849)
species undetermined
n. sp. (New Zealand)
Symplectoteuthis
oualaniensis (Lesson, 1830)
luminosa Sasaki, 1915
Todarodes
filippovae Adam, 1975
Todaropsis
eblanae (Ball, 1841)
Ommastrephes
bartrami (Lesueur, 1821)
Ornithoteuthis
volatilis Sasaki, 1915
Hyaloteuthis
pelagica (Bosc, 1802)
D. Octopodidae
Octopus
adamsi Benham, 1944
australis Hoyle, 1885
cordiformis Quoy and Gaimard, 1832
cyaneus Gray, 1849
duplex Hoyle, 1885
flindersi Cotton, 1932
macropus Risso, 1826
maorum Hutton, 1880
membranaceus Quoy and Gaimard, 1832
pallida Hoyle, 1885
rugosus (Bosc, 1792)
superciliosus Quoy and Gaimard, 1832
tenebricus Smith, 1884
tetricus Gould, 1852
zealandicus (Benham, 1944)
*Hapalochlaena**
lunulata (Quoy and Gaimard, 1832)
maculosa (Hoyle, 1883)

* G. Voss (pers. comm.) believes that *Hapalochlaena* cannot be maintained as a separate genus and intends to incorporate it with *Octopus*.

Recommendations

Since a lack of systematic knowledge is a major impediment to the progress of research on and utilization of cephalopods, I shall make some recommendations that I believe are important for the future of systematic research on cephalopods.

1. First of all, we must put forth the strongest recommendations to increase the financial support for systematic research. Financial support is urgently needed for maintenance of collections and data; for hiring assistants and, especially, illustrators; for costs of publication; for modern equipment, e.g., histological instruments and microscopes; for training students; and for hiring and supporting trained systematists. An impetus to train students, for example, would be recognition by quality universities that systematics is a legitimate science worthy of sustaining advanced degree research. There are major universities in many countries at which theses in systematic topics are not allowed for a doctoral dissertation. Recognition and support by various funding agencies, both basic and applied, as well as a concerted and coordinated effort by existing systematists and by the users or beneficiaries of systematic research, will (or should) provide the persuasion for universities and institutes to offer programs and curricula in systematics. Furthermore, fishery biologists and administrators must recognize that cephalopods represent an exploitable resource with immense potential on a world-wide basis. Cephalopods must be studied in the same manner that all other major fisheries species are studied: the systematics, the whole animal biology, and the populations.

2. Another recommendation concerns the types of specialization required for cephalopod systematics. Training and encouragement are required to develop these specialists.

a. One type is the regional specialist, a scientist who is knowledgeable about the systematics of all species that occur within a region, e.g., Australia, or the Indo-west Pacific. These systematists are necessary to define the fauna that exists within the region, as well as to respond to the requirements of fisheries biologists or biomedical researchers, for example.

b. The other type of specialist is one who studies the systematics of cephalopods at the taxon level but on a world-wide basis. Not only is this approach necessary for the basic science itself, but also it is important to be able to respond on a world-wide basis to the needs of non-specialists with information about particular taxa.

3. A number of useful services or products can be rendered by cephalopod systematists, particularly in the form of publications.

a. Some of the most useful publications, certainly to those who are not authorities in cephalopods, are *keys* to the identification of species. Fisheries biologists, or biologists who study predators of cephalopods, e.g. marine mammals, pelagic birds, pelagic fishes, must know the identity of the species involved in the fishery or as prey organisms. So the recommendation cannot be too strongly made that identification keys be produced as soon as a regional fauna or a taxonomic group is sufficiently known to accurately support such aids.

b. Another aid, to be strongly recommended particularly to systematists themselves, is the *catalogue* that lists the type material or important historical collections that are housed in a particular museum. These are especially important for museums that have large, historically, nomenclatorially important collections, e.g. the British Museum of Natural History and the Museum de Histoire Natural in Paris. While a few catalogues have been prepared (Smith, 1974, California Academy of Sciences; Roper & Sweeney, 1978, National Museum of Natural History, Smithsonian Institution; Zeidler & MacPhail, 1978, South Australian Museum) and one is in preparation for the Zoological Museum, Copenhagen (Knudsen & Kristensen, pers. comm.); catalogues are lacking for all other major collections of the world. Catalogues are extremely useful not only to specialists but to other biologists who may wish to refer to the collections.

c. Finally, publications in the form of thorough systematic *revisions* and *monographs* are the ultimate product of the systematist. Not only do these consist of keys, catalogues, and illustrations, but they should represent the most complete analysis possible concerning the classification, nomenclature, phylogeny, zoogeography, life history, morphology, populations, etc. of the taxonomic group. Because of the breadth of biological topics of a modern systematic monograph, the very strongest recommendation is given for their support and encouragement.

4. A strong need exists to build up authoritative reference collections, particularly in areas where traditionally no sustained cephalopods studies have been conducted, e.g., Australia and South America. Such collections now are needed to support the systematic studies that are increasingly required by fisheries or biomedical researchers, for example. In addition, reference collections should be initiated to encourage deposition of material derived from regional exploratory surveys and local fisheries in order to have available material for the future systematic studies that certainly will be necessary. An example of this type of collection is the Australian Museum in Sydney where for years the need for a reference collection of cephalopods has been recognized and such a collection has been built up, largely as a result of fisheries explorations. Now, with the rapidly developing Australian squid fisheries, much important comparative material is available for the systematic studies that are necessary. Such authoritative reference collections are necessary on national, regional, and world-wide levels.

5. A strong recommendation is given to designate four major families of cephalopods that are in critical need of modern, comprehensive systematic revisions. These are the Sepiidae, Loliginidae, Ommastrephidae, and Octopodidae. They are critical families in that (1) they contain the largest numbers of species that occur in the greatest abundance, primarily in neritic, benthic, or epipelagic habitats; (2) they comprise the great majority of the fishery resource (at least 90%), both currently exploited and potentially; (3) they comprise the species that support biomedical, ecological and other biological research; (4) they are among the most poorly known cephalopods so far as their world-wide systematics is concerned. Researchers, educators, administrators, and funding agencies are urged to recognize the critical status of these families and to encourage and develop the research, educational and financial climate necessary to ensure that these important cephalopods receive the attention required to improve our knowledge and under-

standing. (The Gonatidae and Onychoteuthidae might be added to this list as they are quite speciose and have a potential of significant development in the future).

In view of the status of the world-wide economy it may seem unrealistic to make recommendations that can be carried out primarily through financial commitment. But financial support alone will not advance the science or the development of the resources. Progress in both the scientific and the commercial realms will be achieved only with the combination of financial support and attitudinal commitments. Cephalopods are too valuable a resource for basic and applied purposes for us not to make these firm commitments now for both immediate and future considerations.

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Appendix 2: Bibliography of Cephalopod Biology of the Australian-New Zealand Region

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TECHNIQUES FOR FIXATION, PRESERVATION, AND CURATION OF CEPHALOPODS

CONTENTS

TECHNIQUES FOR FIXATION, PRESERVATION, AND CURATION OF CEPHALOPODS

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I. Introduction

The need for guidelines to techniques of fixation and preservation of cephalopods was recognized at the International Workshop on the Biology and Resource Potential of Cephalopods.[1] It was pointed out that, with a few exceptions, cephalopods traditionally have not been kept in large quantity from biological, fisheries, or environmental surveys. A few representative specimens might have been retained for qualitative (taxonomic) purposes, but this is of little help in retrospective determination of relative abundance, size ranges, maturity levels, populations, etc. To the biologist who is not a specialist in cephalopods the proper fixation and preservation of these animals might seem a difficult task with generally unsatisfactory results. Certainly many poorly prepared specimens exist, but with the increasing interest in the biology and fisheries of cephalopods on a world-wide scale, the necessity and demand for well-preserved material requires that non-specialists be able to fix and preserve cephalopods. Proper fixation is especially important for the identification of species and for biological (e.g., fecundity), histological, and anatomical examination.

We know of no published work that deals specifically with fixation, preservation and curatorial techniques of cephalopods. Although much literature is available for other specific groups of organisms, these techniques do not necessarily apply to cephalopods because of their large size, heavy musculature, lack of a skeleton, etc. The *Unesco* publication edited by Steedman (1976) is an excellent compilation of information for fixation and preservation of zooplankton, some of which is applicable to larger marine organisms including cephalopods. This work is highly recommended for anyone interested in experimenting with techniques of fixation and preservation in cephalopods.

The aim of this paper is to provide guidelines to the techniques of fixation, preservation, and curation of cephalopods for general systematic, morphological and biological purposes. Special techniques, e.g., those for preparation for electron microscopy, are not included. We recognize that we probably have omitted some techniques or chemicals that other biologists have found effective; we therefore solicit suggestions from these workers so that additional material can be incorporated into a future revision of this paper.

II. Materials

II.A. *Fixatives.* Fixation technically is defined as the process of coagulating the contents of cells into insoluable substances (usually by cross-linking proteins) to prevent autolysis and breakdown of tissue (Fink *et al.*, unpublished report, 1979). To be most effective fixation must be accomplished as soon as possible after specimens are captured, preferably on live (sometimes narcotized) material, because cephalopod tissues begin to break down very rapidly upon death. No amount of post-fixation manipulation and treatment will substitute or compensate for correct procedures during the initial phase of fixation. Generally, the process of fixation is accomplished in a relatively short time, usually a matter of hours or days, depending on the size and consistency of specimens and the volume of the fixative. Once proper fixation is achieved a second procedure is performed to insure long-term (permanent) storage of the specimen (i.e., preservation).

[1] The Workshop was conducted at Queenscliff and Melbourne, Australia, 8-14 March 1981.

II.A.1. FORMALIN. Formalin is the fixative of choice for most cephalopod applications. While it is the standard fixative, dilutions vary with different applications. Formalin is prepared by a dilution with water of formaldehyde, an organic compound with the following characteristics:

Formula – HCHO
Molecular weight – 30.03
Boiling point – 19.5°C
Flash point – 30.0°C
Solubility – water, alcohol, ether
Highly reactive; polymerizes readily with various organic materials
Synonyms – Oxomethane, Oxymethylene, Methylene oxide, embalming fluid.

The function of formalin as a fixative appears to derive from the formation of cross-links between adjacent protein chains, resulting in their denaturization and deactivation. Autolysis (self-digestion) is inhibited, and proteins are coagulated; consequently the breakdown of tissues is prevented.

As a fixative for cephalopods, formalin is a dilution of stock formaldehyde (or "full strength" formalin), a 39% by volume (rounded to 40%) saturated water solution of formaldehyde gas. Dilutions vary from 4-10% of the full strength formaldehyde and are prepared in the following proportions:

% formalin	parts formaldehyde	parts distilled water
10	1	9.0
9	1	10.8
8	1	12.6
7	1	14.4
6	1	16.2
5	1	18.0
4	1	19.8

The decision of which dilution to use depends on the size of the specimen(s) and the consistency of the tissues. As a general rule, larger and more heavily muscled specimens require stronger dilutions, up to the 10% maximum. Thus the large, heavy-bodied squids, and octopuses, e.g., loliginids, ommastrephids, onychoteuthids, gonatids, octopodids, should be fixed in 8-10% formalin; medium-sized and muscled forms, e.g., enoploteuthids, histioteuthids, most cranchiids, sepiolids, in 6-8% formalin, and small, thinly muscled or gelatinous forms, e.g., some cranchiids, cirrate and bolitaenid octopods, larvae and many juveniles, in 4-6% formalin.

Because formaldehyde oxidizes rapidly in dilute solutions into formic acid, formalin should be mixed only as it is required, and it should be buffered to maintain near-neutral pH. Formalin undergoing oxidation turns yellow, then red-brown as decomposition progresses. Formalin also interacts with the proteins in animal tissue to form acidic solutions (Taylor, 1977). In cephalopods this acidity will result in dissolution of calcified structures and frequently these very characters are among the most important taxonomic features. Structures most adversely effected by acidic conditions in the fixative (and preservative) include the chitinous sucker rings and hooks, the cuttlebones of sepiids (cuttlefishes), the shells of *Spirula* and *Argonauta*, statoliths, and, to a lesser degree, the chitinous beaks, radulae, and gladii. Acidity also tends to clear tissues and turn them semi-gelatinous. Frequently used buffers include sodium borate (borax), calcium carbonate, and hexamine. A more detailed discussion of buffers appears in a following section.

The amount of fixative used also has bearing on the results. The fluid volume should exceed the tissue volume; a 2:1 to 4:1 ratio generally is sufficient, and never should be less than 1:1.

Duration of fixation in formalin depends on the size and musculature consistency of the specimen and the temperature of the solution. While penetration of formalin is enhanced at warmer temperatures, it is *neither advisable nor recommended* to heat formalin to achieve more rapid fixation. Heating the formalin also will accelerate autolysis and decomposition of the specimen. Large, heavily muscled specimens require longer times for fixation, perhaps several days to two weeks, while small, light-bodied forms are well fixed in one to two days. Specimens should remain in the formalin until the tissues have been completely penetrated and are "hardened". Degree of "hardness" is quite subjective, but experience will indicate the correct stiffness and rigidity. If one is in doubt, it is

better to retain the material in the buffered fixative for a longer rather than a shorter time.

Complete fixation requires complete, preferably rapid, penetration of the tissues. The penetration of formalin is blocked or retarded by presence of lipids in the tissue (Steedman, 1976); therefore, the incorporation of a lipid solvent greatly enhances penetration of the fixative. A suitable solution (Steedman, 1976) consists of:

propylene phenoxetol—1.5 parts
propylene glycol—5.0 parts
formaldehyde (full strength; 40%)—10.0 parts
distilled water—83.5 parts

While this solution is used in preservation of plankton, we are unaware of its application to cephalopods. However, because of the high lipid content in some families, e.g., Ommastrephidae, Gonatidae, we believe this procedure would be worth trying. Empirical observations, in fact, indicate that these are the very families that frequently are the poorest-preserved in collections.

Warning: Formalin in any dilution used for fixation of specimens is noxious at the least and can be dangerous. Extreme care should always be exercised whenever handling or working with this fixative, and vigorous ventilation should be used. Among symptoms due to exposure to formalin are skin, eye, and respiratory irritation, including dermatitis, hives, conjunctivitis, rhinitis, bronchitis, pulmonary adema, headache. Ingestion can cause burning of mouth and oesophagus, nausea and vomiting, abdominal pain, vertigo, unconsciousness. Formalin or formaldehyde is suspected to be carcinogenic in human lungs after long and excessive exposure in industrial settings, but this has not been confirmed (Sax, 1981).

Formalin should be stored in unbreakable containers protected from damage in temperatures not exceeding 16-35°C. It should not be stored in confined spaces or near open flames.

First aid procedures include copious irrigation of eyes with water, washing exposed skin with large amounts of water and soap, and gastric lavage if swallowed, using 1% ammonium carbonate followed by saline catharsis (ITII, 1975).

Spills and leakage should be absorbed with rags and absorbent materials and the area washed down several times with water until the odor disappears. For massive spills, gloves and a gas mask must be used for protection.

II.A.2. BOUIN'S FIXATIVE. This solution is the most extensively used picric acid fixative for general histological preparations. The tendency of picric acid to cause shrinking in tissues is counterbalanced by the swelling affect imparted by glacial acetic acid. Bouin's fixative consists of:

picric acid (saturated aqueous)—15 parts (150 ml)
formalin (full strength =40% aqueous)—5 parts (50 ml)
glacial acetic acid—1 part (10 ml)

Bouin's solution is recognized as one of the best fixatives for general purposes and for histological preparations, because it penetrates tissues rapidly, preserves soft and delicate structures well, and acts as a mordant for certain histological stains. Bouin's solution should be used with soft tissues; due to its high acidity it is not suitable for calcium structures. Also, it destroys red blood cells (not a problem in cephalopods) and cytoplasmic structures, so that cytoplasmic staining is less well defined. Bouin's solution does not interfere with the staining qualities of tissues when the picric acid is removed through successive changes of 70% ETOH. Ideally, Bouin's-fixed specimens (tissue) should be removed and stored in 70% ETOH after fixation is complete.

Since relatively small specimens or individual organs or pieces of tissue normally are fixed, the amount of Bouin's solution used should be at least 10 times the volume of tissue being fixed. Duration of fixation varies between 4 and 24 hours, depending on the size and density of the specimen (tissue). Overfixation or extended exposure in Bouin's solution may cause undesirable effects, so, once fixed, material should be transferred to 70% ETOH. For example, long periods of storage of tissue in Bouin's fixative results in poor staining characteristics of nuclei.

II.A.3. ETHYL ALCOHOL. Alcohols generally do not make good fixatives for cephalopod tissues, but they can be used in an "emergency" in the absence of formalin. Alcohol-fixed specimens tend to become dehydrated and brittle, and they may decompose gradually. If alcohol must be used as a fixative in the field, specimens subsequently can be refixed in the laboratory using the standard buffered formalin technique. Preservation then can be continued in ethyl or isopropyl alcohol.

Ethyl alcohol has the following characteristics:

Formula—C_2H_5OH
Molecular weight—46.07
Flash point—15.8°C (open cup)
Boiling point—78.5°C
Solubility—water, methyl alcohol, ether, acetone, etc.
Highly hygroscopic and volatile liquid; flammable
Synonym—ethanol, ETOH

The hygroscopic property of ethanol allows it to function as a fixative (and preservative) by reducing the concentration of water in cells and tissues. Since enzymatic activity in tissues requires water, the loss of water reduces or stops this activity. Fixation through dehydration of tissues, however, is not as effective or complete as it is through the denaturizing of the adjacent protein chains caused by formalin.

If ethyl alcohol is used as a fixative, it should be in concentrations of 70-75%. Ethanol available for general fixation and preservation is not absolute, that is it consists of 95% alcohol and 5% water. Therefore, to dilute ETOH to 75% requires 3.7 parts of 95% ETOH to 1 part water and a 70% dilution requires 2.4 parts of 95% ETOH to 1 part water. Because ordinary tap water contains impurities that frequently create precipitates that may damage specimens, distilled water should be used for diluting alcohols (Hochberg *et al.*, in press).

A major problem with alcohol as a fixative appears to be its slow and/or incomplete properties of penetration. Specimens, especially those larger than a few centimetres, may appear fixed externally, but their internal structures generally are so poorly fixed as to be nearly indistinguishable because of tissue degradation. The larger the specimen, the poorer the fixation.

The ratio of fluid volume to tissue volume should be as high as possible, at least 4:1 or 5:1, when using alcohol as a fixative, because the water liberated from the specimen(s) significantly dilutes the alcohol. Specimens should remain in alcohol only until they can be refixed in formalin. Acidity may be a problem with long-term storage of specimens, especially with oily forms (e.g., gonatids, ommastrephids). It is recommended that acidity be reduced by several changes of alcohol until the pH approaches neutral (Dingerkus, 1982), but it must be remembered that several changes of alcohol will contribute to excessive dessication of the specimen until it becomes brittle and unmanageable (see Preservation section).

Ethanol is flammable, so it should not be used in enclosed places devoid of adequate ventilation where fumes can build up to the extent that open flame or sparks could ignite them. Irritation of the eyes and respiratory tract can result from exposure to ethyl alcohol fumes; more extreme exposure may produce headache, dizziness, drowsiness, mental confusion, or nausea. Proper ventilation should prevent most fume-induced symptoms. First aid for contamination of the eyes includes liberal irrigation with water and for ingestion, gastric lavage followed by saline catharsis is required.

Fires can be extinguished with dry chemical, alcohol foam, and carbon dioxide retardants (class B and C fire extinguishers). Spills should be absorbed with paper or other absorbant which can be burned.

Stored ethanol must be held in nonbreakable containers in well-ventilated, designated storage rooms, away from all sources of ignition, including static electricity.

A detailed discussion of alcohol(s) appears in the section on Preservation.

II.A.4. FREEZING. Freezing can be a very convenient and effective method of fixing cephalopods, especially large specimens for which no containers are available and in situa-

tions where it is undesirable to have the standard fixatives and preservatives. Best results are achieved with flash-freezing of fresh specimens at −24°C (−10°F) so that the entire specimen is completely frozen before autolysis begins. If possible, specimens should be sealed in air-tight polyethylene bags with the air squeezed out to prevent freezer-burn during storage.

Freezing cephalopods for most biological/systematic uses should be considered only a temporary technique that will fix and preserve the material until it can be fixed permanently in the laboratory.

Techniques for freezing and for thawing frozen cephalopods are given in the Procedures section.

Other Techniques. Several other methods of fixation are used in other groups of animals and are listed here to provide workers with alternative techniques in the event the more preferred techniques cannot be used.

II.A.5. PARAFORMALDEHYDE. Paraformaldehyde has been used in the field for fixing fishes (Fink *et al.*, 1979). It is inexpensive and convenient to handle, as it comes in powder form. A 10% solution is prepared by dissolving 35 g of paraformaldehyde powder in 1.0 l of water (Taub, 1962). To prevent polymerization and precipitation a base, preferably sodium carbonate ($NaCO_3$), should be added to the water which is then heated or boiled prior to the addition of the paraformaldehyde powder.

A 10% solution of buffered formalin can be made from paraformaldehyde by mixing 4 parts paraformaldehyde powder with 1 part anhydrous sodium carbonate, a small amount of powdered wetting agent (e.g., alconox), and 100 parts of water (heating is unnecessary). The powder mixture should be sealed in an air-tight container for storage and transport.

Paraformaldehyde seems to have several advantages over formaldehyde as a fixative: (1) convenience of transport in the field and reduced storage space, (2) no problems with air shipments (1 and 2 refer to the powdered form), (3) purity (stock formaldehyde frequently contains impurities, e.g., methanol, which can adversely effect the specimens). Disadvantages also are noted: (1) a rapid clearing of specimens occurs after preservation (Saul, 1981) when sodium carbonate is used as a catalyst to drive paraformaldehyde into aqueous solution. Paraformaldehyde is difficult to dissolve in water because the powder is a long chain polymer not a crystal. Saul suggests that sodium hydroxide (NaOH) pellets be substituted for the sodium carbonate and that the water be heated or boiled (143 g paraformaldehyde, 7-8 NaOH pellets, 1 gallon H_2O (heated or boiled) = 1 gal. 10% formalin). (2) the pure formalin derived from dissolution of paraformaldehyde is unstable and polymerization occurs with temperature fluctuations, thus inhibiting the fixative properties. There, another chemical, such as a methanol (as in stock solutions of formalin) or ethanol, must be added for stabilization.

II.A.6. GLUTERALDEHYDE. Gluteraldehyde is used as a fixative for preparing specimens (or small pieces) for electron microscopy. This fixative needs to be treated with the utmost care because of its toxic properties. It is a cross-linking agent much superior to formaldehyde. Gluteraldehyde and formalin together appear to create a fixative superior to formalin (Taylor, 1977), but experimentation needs to be carried out on its effectiveness for cephalopods. Apparently gluteraldehyde penetrates well in cool temperatures but not in warm temperatures. Bouin's and Gilson's solutions are used for standard histological preparations.

Certainly other fixatives are available for specialized applications and workers are encouraged to consult modern histological texts and specialists concerning these solutions.

II.B. *Buffers.* A buffer is a chemical system that prevents changes in hydrogen ion concentration. For example, proton donor and acceptor systems act as buffers to prevent marked changes in hydrogen ion concentration. In the context of fixation and preservation buffers are employed to stabilize solutions at an acceptable pH. Both formalin and alcohols develop low pHs, either innately in formalin or in alcohol through exposure to breakdown products from specimens (e.g., fatty acids).

Formalin oxidizes into formic acid and, in the dilute solutions used as a fixative the oxidation takes place rapidly. Also, formalin reacts with proteins leached from specimens to form acidic compounds. Acidic conditions contribute to dissolution of calcified tissues (see section on formalin, above) such as sucker rings and cuttlebones that are important taxonomic characters. Therefore, buffering agents must be added to the fixatives upon preparation to maintain neutral pH. Caution must be exercised, however, because some commonly used buffers such as borax cause adverse effects in specimens, e.g., excessive clearing of tissues (Taylor, 1977). Oxidation can be deterred by filling the specimen container completely to the top, thereby excluding any air/formaldehyde contact.

Alcohols appear to acidify over time for two reasons: (1) oils dissolve out of the tissues and break down into fatty acids, and (2) residual formalin remaining in the specimen from the time of fixation breaks down into formic acid. Initial acidification of alcohol can be prevented by using either distilled or deionized water for dilution or at least tap water with minimal minerals and contaminants. Formalin-fixed specimens should be drained of formalin and rinsed with water to remove all "free" formalin. Specimens should not be soaked to completely remove all formalin from the tissues, as this will lead to deterioration of the specimens. Several changes of alcohol may be necessary in order to achieve neutrality.

II.B.1. CALCIUM CARBONATE. Calcium carbonate ($CaCO_3$) is the buffer of choice for formalin; it occurs naturally as aragonite or calcite. It has several advantages: (1) inexpensive, (2) readily available, (3) does not induce clearing of tissues. Obtainable either as marble chips or marble dust or powder, $CaCO_3$ is added to formalin to excess, beyond a saturated solution, which should maintain a pH of 6.0 (Taylor, 1977). As a buffering agent marble powder is much preferred over marble chips because of its greater surface area and more rapid dissolution that prevents layering of the solutions (Steedman, 1976). It is important to note that Taylor (1977) observed a layering effect of pH in formalin solutions when specimens were fixed (preserved), so that formalin in the bottom of the container had a pH of 6.4, while at the surface the pH was 8.4. Therefore, it is necessary occasionally to invert bottles several times to homogenize the solution or to stir or agitate the solution if fixation is done in trays or basins.

II.B.2. SODIUM BORATE. This base, often called borax, is a commonly (and traditionally) used buffer of formalin used for fixation. The formula for sodium (tetra) borate is $Na_2B_4O_7 \cdot 10\ H_2O$. It is more soluble in water than $CaCO_3$.

A "rule of thumb" indicates that sodium borate powder should be added to the undiluted formaldehyde until saturation is achieved, a 1 to 2% solution, giving a pH of 8.0-8.3. But this may be excessive for other reasons, since even when diluted it causes lysis of tissues and clearing of pigments within 1-2 years (when formalin is used as the preservative) and this effect may be more undesirable than slightly acidic conditions. So borax should be used only for short periods of time. A less concentrated solution can be made by dissolving 5 g of sodium borate in 1.0 l of full-strength formalin. This should suffice for short-term neutralization (a maximum of 1 year). Borax that has been added to saturation eventually will precipitate out as white, sticky globules that may adhere to specimens and obscure the finer morphological details.

II.B.3. HEXAMINE. Hexamine, $C_6H_{12}N_4$, is an organic compound also known as hexamethylenetetramine, urotropine, and methenamine (molecular weight 140.19). As a formalin buffer, hexamine maintains a stable, non-acidic pH of near 7 (depending on solutions used), a level not achievable with chalk or borax. A solution of 200 g of hexamine in 1 litre of full strength formalin should provide a constant neutrality (pH 6.2 to 6.9) of the 10% formalin fixative diluted with distilled or sea water. That is, the final dilution in 10% formalin would be 2% hexamine. Hexamine works in 3 ways in formaldehyde solutions: (1) as a mild base, (2)

as an anti-oxidant, (3) to remove acid in solution (Smith, in Steedman, 1976).

Concentrations above 2% are not advisable as they may result in damage to the specimens by softening and swelling of proteinaceous tissues. Warm storage conditions also will cause degradation of calcareous tissue, therefore cool to cold conditions are recommended.

While a number of compounds will buffer fixatives and preservatives to pHs well above 7, the concentrations required to maintain neutral or above pHs in themselves are deleterious to animal tissues, as is the case with borax and hexamine.

II.C. *Preservatives.* Preservation is the process of permanently maintaining the fixed state of specimens and tissues. Several chemicals are used as preservatives and in general they are less toxic (therefore less dangerous for people to work with) and they avoid the harsh side effects of initial fixatives (e.g., the decalcification of hard tissues caused by formalin). The most common preservatives for cephalopods are ethyl alcohol, isopropyl alcohol, and formalin. The decision about which chemical to use is typically based on a number of factors: (1) availability, (2) cost, (3) tradition, (4) regulations, (5) human considerations (e.g., allergies), (6) type of material (e.g., size and consistency of specimens), (7) anticipated use of material, etc.

Interestingly, no long term comparative experiments have been conducted to determine objectivity which preservative is the best for permanent preservation of cephalopods. While for most applications alcohol is accepted as superior to formalin for preservation, little experimental information exists to indicate which alcohol, ethyl or isopropyl, is superior. Whichever preservative is used, it should have the following characteristics:

(1) provide permanent preservation so that material is available in a state suitable for systematic and specimen-oriented examination by future generations of researchers.

(2) allow as many systematic (taxonomic) characters as possible (ideally all) to be preserved.

(3) allow as many biological and anatomical features as possible to be maintained, e.g., spermatophores, ovaries, photophores, internal organs and systems.

These characteristics imply that acceptable preservatives should not: dehydrate or distort soft tissues; decalcify, distort, clear, or dissolve hard tissues; allow biological or chemical activity to occur (e.g., bacterial growth, autolytic enzyme activity or acidification).

II.C.1. ETHYL ALCOHOL. Ethyl alcohol (or ethanol or ETOH), C_2H_5OH, molecular weight 46.07; boiling point 78.5°C traditionally has been the preservative of choice for cephalopods in concentrations of primarily 70 to 75%. It has several advantages over isopropyl alcohol, the other alcohol preservative used for cephalopods (see below): (1) it is relatively more pleasant to work with, both in odor and effect on skin, (2) specimens are firmer, (3) the higher concentrations used, 70-75%, reduce concern of dilution below levels safe for preservation, (4) specimens in ethanol are preferable for most histological techniques.

Several disadvantages also are noted for ethyl alcohol: (1) the higher concentrations of ethanol result in a greater rate of evaporation especially if air space occurs between the surface of the fluid and the closure of the bottle and if closures are inadequate, allowing leakage of evaporated alcohol, these effects result in the necessity for greater curatorial attention, (2) specimens are more dehydrated in 70-75% solutions, consequently are harder and more brittle, especially if alcohol must be added or changed, (3) when tap water or sea water is used for dilution an undesirable precipitate may be formed; so distilled or deionized water is necessary, (4) ethanol is very flammable (flash point 15.8°C, open cup) so great caution is required in the storage of undiluted alcohol, and even with diluted solutions in the collections area and laboratory, (5) it tends to be more expensive than isopropanol, (6) since ethanol is a stimulant and intoxicant its purchase, handling, and use are rather strictly controlled by Federal and State regulations which require a considerable amount of records-keeping and secure, fireproof storage facilities.

Permanent preservation of well-fixed

cephalopods in ethanol requires a volume of alcohol to volume of specimen(s) of at least 2 to 1 (33% specimens) and preferably greater, e.g., 3 to 1 (25% specimens). Practical considerations of availability of large containers or of storage space may force the use of containers too small for the size (volume) of the specimen(s). In such cases frequent checking of the material is mandatory to ensure that fluid concentrations do not drop. Alternatively and preferably, if more than one specimen is involved, the lot should be divided into several containers (appropriately labelled). Since the free water content of the specimens dilutes the alcohol significantly, one or more changes of alcohol may be necessary to bring the concentration up to the desired permanent strength. The final (shelf) concentrations of alcohol that result from initial preservation with subsequent changes of alcohol were calculated by Taylor (1981) for three different volumes occupied by specimens and two different water contents of the tissues. The results of which are presented below:

Volume of specimens in container	25%		50%		75%	
Water content of specimens	65%	90%	65%	90%	65%	90%
Alcohol percentages after the following changes:						
Add 40% alcohol	32.9	30.8	24.2	21.1	13.6	10.8
Change to second 40% alcohol	38.7	37.9	33.8	31.0	22.5	18.7
or						
Add 75% alcohol	61.6	57.7	45.5	39.5	25.4	20.3
Change to second 75% alcohol	72.6	71.0	63.4	58.2	42.2	35.1

Clearly, high water content of tissues and high specimen volume in containers result in dangerously low concentrations of alcohol.

Taylor also calculated alcohol contents resulting from a system of three successive changes of increasing concentrations of alcohol (35%, 55%, 75%), but in general this technique does not yield as high final percentages as the methods in the table above. The topping up of bottles in which evaporation has occurred is discussed below.

Acidity is a problem in alcohol-preserved specimens as well as in material fixed or held in formalin. The acidity causes brittleness, especially in specimens with high oil content (e.g., ommastrephids, gonatids). The oils dissolved out of the specimens in alcohol, primarily from the digestive gland or "liver", break down into fatty acids. Acidity also may be caused by the residual formalin that remains in the specimens after initial fixation breaking down into formic acid. For example, a test solution of 1% formalin in 50% isopropyl alcohol was nearly neutral (pH 7) at mixing but dropped to pH 5.5 within one month (Dingerkus, 1982). Therefore, formalin-fixed specimens must be drained and rinsed in freshwater, with all residual formalin and rinse water drained from the mantle cavity, prior to placement in the alcohol preservative.

To prevent or reduce acidity one or more periodic changes of alcohol may be necessary before the final preservation, but since dehydration of tissues also may be a problem with 70-75% ethanol, the addition of a nonclearing buffer (e.g., hexamine, not borax) might be preferable to several changes of alcohol. Alcohol should be diluted with distilled or deionized water to avoid initial acidification and precipitate formation.

Some workers suggest adding a small amount of glycerine (glycerol) to the alcohol to prevent hardening and brittleness in specimens. Also, propylene glycol (1-2 propanediol; $CH_3CH(OH)CH_{20}H$) can be used as an additive (2-5%) to formalin fixatives and preservatives and to alcohol preservatives to promote softening of fixed protein and to maintain flexibility of tissues (Steedman, 1976). It also appears to promote penetration of formalin as a fixative (in combination with propylene phenoxetol) and to inhibit growth of molds. We have no direct experience with these softening agents, but we encourage experimentation.

II.C.2. ISOPROPYL ALCOHOL. Isopropyl alcohol has become more frequently used as a preservative for cephalopods in the last decade or so. Isopropyl alcohol $(CH_3)_2CHOH$, has a higher molecular weight (60.09), a higher boil-

ing point (82.4°C) and a higher flash point (21°C, open cup) than ethanol. Isopropyl alcohol also is known as dimethylcarbinol, as well as isopropanol.

The advantages of isopropanol over ethanol include: (1) it is relatively inexpensive both in initial purchase cost and because it is used in greater dilutions, (2) it is less volatile, therefore evaporates less, does not desiccate tissues as much, and is less of a fire hazard, (3) it is not regulated as stringently by Federal and State agencies so there are fewer records-keeping, storage, and security requirements, (4) tissues are softer and more pliable, thus easier to work with, (5) lower concentrations (to a point) are adequate for long-term preservation without inducing desiccation.

Disadvantages associated with isopropyl alcohol in comparison with ethyl alcohol include: (1) it is noxious and relatively unpleasant to work with; adequate ventilation is required (adverse symptoms are conjunctivitis, corneal ulceration, skin irritation, headache, and nausea from fumes and decreased blood pressure, nausea, vomiting, haematemesis, anuria, uremia, hepatomegaly, and anaemia from ingestion; excessive exposure in career-long industrial production may cause carcinogenic effects in respiratory tract, ethmoid sinus, lungs, larynx, and paranasal sinuses (Sax, 1981)), (2) concentrations below 45% may cause degradation of specimens including clearing and disintegration of tissues, possibly the result of reactivation of autolytic enzymes in the cells (refixation and restoration of 50% concentration should solve the problem), (3) it is not highly soluble in water, so unless great care is taken to thoroughly mix the solution, layering will occur in the container inducing degradation of tissue near the bottom and increased evaporation from the higher concentration at the top, (4) once mixed it is difficult to measure solution strength because the specific gravity of isopropanol is very close to that of water, (5) impurities in stock alcohol may induce clearing of tissues (i.e., some drums may have contained other chemicals prior to alcohol), (6) dilution with tap water ("hard" water) causes a precipitate to form on the specimen or in the bottom of the container; this is remedied by using distilled or deionized water, (7) specimens and tissues preserved in isopropanol are unsuitable for histological purposes.

Cephalopods have been preserved in different concentrations of isopropanol: 40%, 45% and 50%. Recent observations, particularly in fishes (many of which have tissues of comparable consistency, thickness, and texture with cephalopods), indicate that a 50% solution gives superior preservation; lower concentrations will be diluted by the free water in the specimens to levels considered unsafe for preservation (Taylor, 1981). On the other hand, some workers have reported that tissues become stiff and brittle at isopropanol concentrations of 55% and above. Therefore, a 50% solution of isopropanol is recommended for preservation of cephalopods.

Information given in the section on ethanol concerning specimen to fluid volume ratio, acidity, changing fluids, etc. is applicable to isopropyl alcohol.

II.C.3. FORMALIN. The characteristics of formalin were discussed in detail in the section on fixation. While formalin is considered the best fixative for cephalopods, it is not regarded as a good long-term preservative. It has strong disadvantages: (1) it is noxious, allergenic, toxic, and possibly carcinogenic, so working on formalin-preserved specimens is very unpleasant, (2) it turns acidic through oxidation and through interaction with proteins from the specimens, causing decalcification of chitinous tissues, degradation and clearing of soft tissues, and eventual disintegration of the specimen.

Advantages of formalin as a preservative are difficult to find. However, it is inexpensive and standard dilutions in water yield osmotic pressures close to sea water so it can be used as a temporary preservative especially in the field where alcohol might be unavailable or undesirable for some reason. Since it can be made from powdered paraformaldehyde, its use greatly reduces the weight and bulk associated with solutions of formalin and alcohol (at least going into the field). It must be stressed very strongly that all formalin used as a preservative must be buffered, just as is

necessary when used as a fixitive. Calcium carbonate in the form of marble dust appears to be the best buffer for this application. Containers should be completely filled and tightly sealed so no air comes in contact with the formalin to induce oxidation and acidification.

Concentrations will vary according to specimen consistency, size, etc. (see section on Fixation) but should never exceed 10%; even for short-term preservation a maximum of 8% should be sufficient (a maximum of 6% for eggs, larvae and gelatinous forms). If specimens are to be retained in formalin for temporary preservation, they should be changed from the initial fixative solution into a fresh, generally more dilute, buffered solution.

II.C.4. FREEZING. Freezing is recognized as a good technique for keeping cephalopods under unusual circumstances (see section on Fixation). However, it generally cannot be recommended for permanent preservation, unless, again, unusual circumstances necessitate it and special caution is exercised. For example, formalin and alcohol might be unavailable, the specimen(s) might be too large or too numerous for any available containers. Freezing should be achieved as quickly and thoroughly as possible to prevent tissue degradation, e.g., by the "flash" technique, and the material should be retained at temperatures low enough to prevent the slightest possibility of thawing.

Specimens to be fixed and preserved by freezing must be sealed in polyethylene (plastic) bags if at all possible to prevent the dehydration and "freezer burn" inherent with unprotected frozen specimens.

The following section on procedures explains how to properly thaw and fix specimens initially fixed by freezing.

II.D. *Containers.* The kinds of containers in use to store cephalopods are as varied as the countries and institutions which house them. The storage container which has the longest shelf life and requires the least amount of curation is a clear glass jar with a rubber gasket and glass lid sealed with a wire clamp-top (bail top). Other types of containers have drawbacks, such as the "backing-off" of screw top lids caused by temperature fluctuations, rusting of metal lids, distortion of paper liner in some screw top lids and the eventual breakdown of some types of plastic jars and lids caused by the alcohol.

Any weakness in the type of container used eventually will lead to evaporation of the preservative and degradation of the specimen. If topping up of the preservative is required, the % alcohol and pH first should be determined to ensure that the strength of the preservative to be added will return the solution to its proper concentration and pH. Several techniques have been used with varying success to try to reduce the amount of evaporation from screw-top containers, such as parafin wax and sealing tape. These have the drawback of having to be redone every time the container is opened.

Currently the cephalopods at the National Museum of Natural History are preserved in the following range of sizes and types of containers: 2 and 4 ounce glass jars with plastic screw tops and conical plastic liners; 8, 12, 15, and 32 ounce glass jars and lids with metal, bail-top closure and rubber gaskets; 1, 2, 3, and 5 gallon glass buckets with plastic lids and plastic liners, $14 \times 16 \times 18$ inch and $14 \times 16 \times 36$ inch stainless steel tanks and lids with rubber gaskets and snap closures; and finally, $2 \times 3 \times 5$ foot marine plywood tanks lined with fibreglass (each contains three stackable PVC plastic trays constructed with stainless steel rivets).

II.E. *Labels.* Labels are an overlooked but critical component of curation. A rare or important specimen obtained through expensive ship-collecting techniques can be rendered almost useless by a disintegrated label. Formalin, and even alcohol, can completely digest some papers. Labels should be made of 100% rag paper with a high wet fibre strength. An alternative to this type of paper is currency paper which also has a high wear property. A permanent, waterproof India ink is recommended for writing. The high carbon, black inks which are indelible in formalin and alcohol provide the high contrast and permanency required for a museum or reference collection label. Ball point and fountain pen inks should never be used as the ink will dissolve in alcohol. Soft lead pencils are an acceptable alternative

for writing field labels but are not recommended for permanent labels. Typed labels cure the problem of illegible writing providing the ink is indelible in formalin and alcohol. When in doubt, always test the label paper and ink to be used in the fixative and preservative for several days to assure permanency.

Field labels should be made from the high quality paper described above, 100% rag. Very often the amount of time that elapses between the writing of the field label and the insertion of the permanent label is much longer than is anticipated. Also for this reason the data included on the label should be as complete as possible. Minimum data for field labels should include collector, station (or field or other identification) number and date collected. A preferable amount of collecting data for field labels would be collector, station number, date collected, geographic location or latitude and longitude (for oceanic localities). A log book always must be compiled with all pertinent collection data at the time the field labels are written.

Permanent labels should be generated once the material is transferred from the fixative to the preservative. These labels should include all known data pertaining to the specimen, including collector, station number, date collected, geographic location or latitude and longitude, depth collected, habitat, collecting gear (method), preservative and eventually identification of specimen(s), name of identifier, number and sex of specimens and some sort of catalogue or index number.

III. Procedures

III.A. *Prefixation Preparation of Specimens.* Before cephalopods can be fixed and preserved they require a certain amount of preparation to ensure maximum quality for systematic and morphological uses. Techniques vary with the size, structure, and number of specimens, the method of capture, and the state of the unfixed material (e.g., live, fresh-dead, long-dead, frozen). Of course, all specimens should be fixed as soon after capture as possible, because autolysis and decay processes commence at death.

III.A.1. DEAD SPECIMENS. Cephalopods captured in trawls or other moving collection devices (as opposed to traps and wiers, for example) generally are dead by the time they come on board, unless special techniques are employed to secure living material. Freshly dead specimens, regardless of how they were captured, must be handled very carefully because they are fragile; rough handling will tear integument and obliterate color patterns, rupture eyes, break off tentacles and arms, dislodge light organs, etc. Specimens should be placed into a tray, basin, or other container large enough to accommodate both the size (length) and numbers of specimens to be fixed. It is important to lay out the specimens so that the arms extend anteriorly and are not twisted and knotted, the tentacles, if longer than the arms are turned back along the head and body, the body and head are aligned, not bent and twisted; specimens should look as natural as possible.

III.A.2. LIVE SPECIMENS (NARCOTIZING). Specimens captured alive generally must be narcotized or killed prior to fixation to prevent contraction and distortion of arms, tentacles, mantles, which make the specimens very difficult to work on. Live specimens simply dropped into the fixative may contract so violently that their mantle openings are sealed and do not allow the fixative to bathe the mantle cavity and internal organs; heavily muscled forms may decay or autolyze internally before the formalin penetrates the mantle. Octopuses dropped into formalin alive will contract their arms so violently that they become rigid coil springs. Larval and juvenile cephalopods contract their heads into the mantle cavity, distorting the internal organs.

Narcotizing may be accomplished in several ways, but it must be emphasized that all techniques should be accomplished slowly so as not to disturb the specimen during narcotizing.

The objective of narcotizing is to get the specimen so relaxed and insensitized that it will not react by contracting at the introduction of the fixative. Since narcotics can lead to death (then rapid onset of decay), care and experience are required to determine when the animal is still alive, but sufficiently narcotized to be fixed; this can be done by probing the specimen with a

dissecting needle or glass rod. A great deal of experience and experimentation are required in using narcotizing reagents because different species and sizes (ages) react differently to different (or the same) reagents.

1. Ethanol is an effective narcotizing agent on cephalopods. Pure 95% alcohol is added slowly to the sea water until a 0.5 to 1.0% solution is reached; narcosis is achieved at a rate proportional to the size of the animal, generally within 1-2 hours. Since ethanol in these concentrations is not toxic, narcotized specimens can be operated on and manipulated; recovery is induced by placing the specimen back in pure running sea water. Or, if fixation is desired, the specimen can be fixed when it no longer reacts to gentle stimulation with probe or glass rod.
2. Cold water serves well as a narcotizing agent, especially on tropical forms. Lower the temperature of the water that contains the specimen gradually to 4°C. If narcosis is not satisfactory, the temperature can be lowered to near the freezing point of sea water: −1.9°C.
3. Decreased salinity has proven effective in narcotizing octopuses. Salinity is reduced gradually over a period of several hours until it reaches ½ normal salinity (i.e., 17 to 18°/₀₀). By this time the specimen is so lethargic that its sensitivity can be tested by probing or handling. Special techniques still are required for fixation, however, to prevent the arms from becoming coiled and distorted (see following section).
4. Magnesium chloride isotonic with sea water, $MgC_{12}\cdot 6H_2O$, works well as a narcotizing agent on other molluscs, including adult bivalves, in the ratio of 7.5 mg $MgC_{12}\cdot 6H_2O$, 92.5 ml distilled water, 100 ml sea water. We are unaware of its use on cephalopods, but it would be worth experimenting with if the other techniques fail.
5. Urethane (Ethyl carbamate, $NH_2\cdot COOC_2HS$) has been used to anaesthetize octopods prior to surgery (Boycott & Young, 1955). Urethane is now suspected to be a carcinogen and should not be used.

III.A.3. PHOTOGRAPHY. The color and color patterns of cephalopods are important features that are not retained well in preservation, because the pigments in the chromatophores are denatured by the fixative and preservative. Therefore, notes on coloration and color photographs are especially desirable documentation obtainable only when the animal is still alive or very freshly dead. Chromatophores may remain active for some time after the rest of the animal is dead, but they show only color, not the full array of color patterns of the live specimen. Photographs should be taken of the dorsal and ventral surfaces of each fresh specimen that has been laid out in a "natural" position in a tray. Close-up shots should be taken of special features, such as the ocelli on octopuses and color patterns in squids. Specimens should be in water when photographs are taken to eliminate reflections from the smooth surfaces. A size scale in the photo is recommended. A log should be kept of each (series of) photo(s) listing the state of specimen (alive, narcotized, fresh-dead, etc.) and any pertinent data that will identify the photo with the specimen at a later date.

III.A.4. ORIENTATION OF SPECIMENS. Prior to fixation, dead or narcotized specimens must be oriented properly so that they will be fixed in a position that will be most useful to the researcher. Specimens are laid out in a plastic or enamel tray or basin so that the body and head are aligned with no bends or twists, the arms are extended anteriorly and parallel to each other, the tentacles, if longer than the arms, are turned posteriorly along the side of the head and mantle.

III.B. *Fixation.* The fixative, e.g., 8% formalin, is added carefully until the specimens are completely covered; volume of fixative to volume of tissue ratio should be 2:1 to 4:1. If larger specimens are fixed on a rolling vessel they can be kept in proper orientation with cheesecloth or towelling placed loosely around them, *not* tightly wrapped, as this will retard fixation and specimens will be fixed with any

pattern or wrinkles that is in the covering material.

Cephalopod eggs and eggs masses are fixed in 4% neutral formalin or in Bouin's solution. For this material 70% ethanol is a poor fixative. If the eggs are embedded in a tough coating or matrix they should be opened to ensure good penetration of the fixative.

Larval, juvenile and small adult specimens up to about 20-30 cm total length and gelatinous, soft bodied specimens of any size, can be fixed as they are, but larger specimens, especially those heavily muscled forms (e.g., ommastrephids, onychoteuthids, gonatids), should be cut open to allow penetration of fixative into the mantle cavity. Start the incision several centimetres posterior to the mantle opening (to prevent the mantle from being fixed as an open, flat slab) and continue along the ventral midline to a point several centimetres anterior to the tip of the tail. The incision should be made only through the thickness of the mantle to avoid damage to the internal organs, some of which press against the inner surface of the mantle. If any pattern of chromatophores or photophores occurs along the ventral midline, the incision should be made slightly lateral to the midline to prevent damage. On large specimens with necessarily long incisions it may be necesary to tie thread around the mantle to maintain its cylindrical shape as much as possible, while leaving the slit gaping enough to allow penetration of the fixative.

Very large specimens, e.g., large *Dosidicus*, *Ommastrephes*, *Moroteuthis*, *Architeuthis*, should be injected in the head and body with formalin to ensure fixation of tissues. Long, large diameter syringe needles are recommended.

Eggs, larvae, and soft bodied juveniles should be fixed as soon as possible in: (1) 4% neutral formalin for a period of 12 to 24 hours and then preserved in 70% ethanol. Note—it is very important to include the method of fixation and preservation on the lable (S. v. Boletzky, pers. comm.). Larger and more heavily muscled forms require proportionally more time in the fixative, up to (8% formalin) a maximum of two weeks for the largest, heavily-muscled specimens; acidity must be (2) rigorously controlled at neutrality, which will require periodic changes of buffered fixative.

How many specimens should be fixed? Frequently this is a question that poses no concern because only one of a few specimens of each species are available and all should be fixed. But in survey work samples may contain many hundreds of specimens usually of the same species. When samples (stations) are very close in space and time, a minimum of 7-10 specimens per species should ensure that at least both sexes are represented; a few more are necessary if a significant size range occurs. If samples are separated in space and time, 25-50 specimens should be fixed to ensure an accurate representation of sizes, sexes, species, etc.

Special problems. The arms of octopuses, especially, are prone to coil tightly during fixation if the specimen is alive and unnarcotized. It is extremely difficult to identify and study specimens with coiled, contracted arms. Therefore, it is recommended that octopuses be dead or heavily narcotized before fixation. Narcotization in gradually diluted sea water works well (see section on narcotizing). During late stages of narcosis the arms should be stroked and pulled out straight. During fixation the arm tips are first immersed in fixative then removed and stroked straight. This process is continued gradually until the whole length of the arms has been dipped in fixative. The specimen is laid in the tray with the arms arranged out straight. Further stroking might be necessary as the formalin penetrates the muscles of the arms or the arms can be rolled in paper to form a supporting tube. Although time-consuming, these procedures ensure high quality fixation. If many specimens are to be fixed, at least a few should be fixed in this manner.

III.C. *Transfer from fixative to preservative.* The method of transfer to preservative depends on whether the specimen has been fixed or frozen.

III.C.1. FIXED SPECIMENS. Transferral of cephalopods from fixative (formalin) to preservative (alcohol) is a relatively simple procedure, as stepping them up through a graded series of

alcohols generally has not been considered necessary. However, recent research indicates that one or two changes in alcohol will ensure removal of the free water in specimens that dilutes the alcohol. Specimens should not be transferred to alcohol if histological work is anticipated, but it is recommended to transfer specimens from the original formalin fixative to a fresh solution of strongly buffered (neutral, pH7) formalin; a slightly reduced concentration from that of the original fixative is recommended.

Specimens should be removed from the formalin and all fluid drained out of the mantle cavity. Specimens then should be gently rinsed off and the mantle cavity flushed out with fresh water to remove any free formalin, but cephalopods should *never* be soaked or washed over a period of time to remove most or all traces of formalin. The small amounts of bound or residual formalin in the tissues will enhance storage life so long as the alcohol does not become acidic. Most specimens can be transferred directly into 75% ETOH or 50% isopropyl alcohol, but especially gelatinous or "watery" material should be stepped up (several days at each step) through a graded series of alcohols, e.g., 35%, 55%, 70%, and 75% for ethanol and 20%, 30%, 45%, and 50% for isopropyl alcohol to eliminate or reduce the probability of shrinkage and distortion of the tissues. Especially important specimens of any consistency, e.g., types or those to be used for anatomical or morphological dissections, also should be run up through the alcohol series. Alcohols should be buffered to prevent acidification (see above).

Preserved collections must be periodically inspected to ensure that alcohol levels and concentrations are maintained. With proper bail-top closures or with soft plastic lids (polypropylene) and polyethylene disc liners on bottles (see above) an annual inspection should be adequate. But if metal, bakelite, or other plastic (phenolic or polystyrene) lids are used with cardboard or foil liners it will be necessary to check alcohol levels more frequently.

When evaporation has occurred the alcohol must be restored, but problems arise with simply "topping up" the bottle. During evaporation the more volatile alcohol goes off leaving a dilute alcohol solution or in severe cases only water, so topping up with the normal concentration (50% isopropanol or 75% ethanol) will not restore the solution to the correct shelf concentration. Topping up with a higher than standard concentration will help, but unless actual concentrations are measured, the strength will not be known. An alcohol hydrometer should be used to measure the concentrations to ascertain whether they are too low or high. Successive topping up over a period of years will lead to ever-increasing dilutions. So, if more than 10% of the solution in the bottle has evaporated, it is recommended that the fluid be replaced entirely. If topping up is the only recourse (because of the financial burden of replacing the alcohol, for example), it should be done with a stronger solution than the shelf concentration, say 80-85% ethanol or 55-60% isopropanol, depending on the amount of evaporation.

III.C.2. FROZEN SPECIMENS. Frozen specimens must be thawed before they are fixed and preserved. Specimens placed in fixative while completely frozen will be fixed in their frozen shape and configuration, usually quite distorted. Also, external tissues will be fixed as they thaw, while the retarded thawing of internal tissues may prevent their fixation, because penetration of fixative will be inhibited by already fixed outer tissues. Further, the effectiveness of formalin as a fixative is suppressed at low temperatures.

Frozen specimens should be thawed slowly either at room temperature or in a polyethylene bag in warm (never hot) water. When specimens are soft and pliable, but *not completely thawed*, they should be oriented properly, especially the arms and tentacles, and fixed according to standard procedures (see above). Completely thawed specimens, especially the internal organs, become very soft and quickly lose their structural integrity, so that even subsequently properly fixed they are poor specimens. Also, the sucker rings and/or hooks on the arms and tentacles are lost from the thawed, relaxed suckers. So, such specimens are of reduced value for taxonomic and anatomical purposes.

III.D. *Packing and Shipping.* The method of packing depends on the quantity (i.e., size and weight) of material and how it is to be shipped. Small specimens (e.g., most of those caught in nets the size of a 3 m Isaacs-Kidd midwater trawl) and lots with few specimens should be sealed in a polyethylene bag with a volume of fluid twice that of the volume of the specimens. The bag then should be sealed in a second bag to prevent desiccation of the specimen(s) in the event of leakage. If weight, thus cost of shipping, is a major concern, the specimens should be wrapped in cheesecloth, placed in the polybag, saturated with preservative and sealed in the two bags. The bagged specimens are carefully packed in a liqui-pack or other strong shipping container (preferably one that retains fluids) with appropriate cushioning materials. If a leak-proof container is not available, a large polybag (e.g., trashbag) should be used as a liner for the shipping carton or crate. Polybags should never be overcrowded in the shipping container so that those on the bottom become mishappen, crushed, or ruptured.

Large specimens must be thoroughly wrapped in cheesecloth and saturated in preservative. They may then be double bagged or if too large, placed directly into a liquid retaining container with additional preservative.

Very small or delicate specimens and important museum specimens (e.g., types) frequently are shipped in glass containers. These vials and jars must be individually wrapped in some type of cushioning material (e.g., "bubble-sheeting"), and packing material must be placed around all interior surfaces of the shipping container. It is also a good practice to cushion the specimen within the jar. When in doubt always use additional protection for the specimen and the strongest shipping container available. The roughest treatment specimens receive occurs during shipment from one location to another. Always be certain to include a proper label in each polybag, vial, or jar of specimens. An invoice listing all lots should be enclosed in the shipping container. If the specimens are to be shipped internationally, a label on the outside of the shipping container should state that the contents are "preserved biological specimens of no commercial value".

IV. Chitinous and Calcareous Structures

Several calcareous or chitinous anatomical structures must be removed from cephalopods for specific taxonomic purposes, and it is important that they be preserved properly for future reference. These features include the gladius of squids, cuttlebone of cuttlefishes, beaks, radulae, and statoliths. The techniques for removal or extraction of these parts and for their preservation are presented below.

IV.A. *Gladius.* The chitinous gladius or pen lies below or partially embedded within the mantle musculature along the dorsal midline of squids. Two procedures are used for extracting the gladus from fresh and preserved specimens, the first being recommended for most species (Toll, 1982).

1. Ventral. The mantle is cut open along the entire ventral midline. The left gill is cut from the mantle wall along the gill membrane and the stellate ganglion is severed either proximally or distally. The left lateral edge of the free rachis is freed anteriorly from the surrounding tissue; then, working posteriorly, the remainder of the gladius is freed from the shell sac with particular care being taken to prevent damage to the delicate posterior tip where a conus may be present. The viscera are reflected toward the right side away from the gladius and the gladius is lifted out.
2. Dorsal. In species that have incomplete mantle musculature across the dorsal midline (e.g., Onychoteuthidae) the midline of the gladius lies exposed beneath the dermal layers. An incision is made along the entire dorsal midline taking care not to cut into the gladius. The cut edges of the mantle are reflected laterally and the gladius is freed along its edges and lifted straight up out of the shell sac and mantle.

The removed gladius is best preserved with the specimen from which it was taken, either by replacing it into the shell sac and tying the mantle closed with thread or by placing it in a long vial or tube closed with a sponge plug. The

gladius should not be put in the bottle without protection as it might be damaged. The gladius also can be tied gently between glass slides or plates, with shims or spacers to prevent flattening. Gladii should never be dried as they distort, become very brittle, and break easily.

IV.B. *Cuttlebone.* The cuttlebone in cuttlefishes (Sepiidae) is the homolog of the gladius. It is calcareous and easily damaged, especially the posterior spine and conus, but because it has such important taxonomic value it frequently must be removed to identify the species. An incision is made with scissors along the entire length of the dorsal midline through the thick dermal layers (generally no mantle musculature extends across the cuttlebone), the edges of the incision are spread apart, and the chitinous edges of the cuttlebone are teased away from the shell sac. Particular care is required to free the conus/spine posteriorly. The cuttlebone then is lifted out of the sac.

The calcium carbonate composition of cuttlebones makes them very susceptible to dissolution at reduced pH. So every effort must be made to maintain neutrality and prevent acidity through addition of a buffer to the fixative and preservative (see above). Cuttlebones can be preserved with the specimens from which they were removed, but if any doubt exists about maintaining neutrality of the preservative, they should be preserved dry. The cuttlebone should be rinsed thoroughly in fresh water, drained and air dried. Some cracking of the chitinous edges will occur. It should be stored in a covered specimen box or tray, in a capped bottle, or in a "zip-lock" plastic bag properly labelled with complete data so it can be identified with the animal from which it was taken. Cotton should be placed at the posterior tip to prevent damage to the spine and/or conus in the box, or placed in the bottom of the bottle, where the anterior end of the cuttlebone is placed; the upward-pointing posterior end also should be protected with cotton.

IV.C. *Beaks.* Several techniques exist for extracting the chitinous beaks (jaws, mandibles) of cephalopods.

1. Beaks are easily removed from freshly dead, thawed, or stomach-content specimens by gently teasing them out of the muscular buccal mass. The lower beak should be removed first. If any resistance is felt when the beaks are pulled with forceps or fingers the muscles should be cut carefully from the edges of the wings, hood and lateral walls.
2. Beaks are much more difficult to remove from preserved specimens, so they must be dissected from the buccal mass by careful cutting along the surfaces of the wings, hoods, walls, etc. Soaking in fresh water for several days will help soften the muscular tissue. Excess tissue can be carefully scraped from the extracted beaks.
3. Chemical techniques frequently are used to extract beaks from the buccal mass, but they often are so traumatic that they distort or damage the beaks of some species. We suggest that chemical methods be tried on one specimen before subjecting others to possible damage. The results of chemical cleaning may vary depending upon the species and age of the specimens.
   a. Trypsin. Trypsin is a naturally occurring proteolytic enzyme. To make a saturated solution of Trypsin in distilled water (allow 1-2 days to insure complete saturation), mix 3 parts Borax and 7 parts distilled water with 1 teaspoon trypsin. Trypsin must be stored dry in a sealed container and refrigerated. Very little of the powdered trypsin will go into solution, so large amounts will not increase the masceration of tissue. Place the extracted buccal mass in the solution for 1-2 days until the tissue is softened or dissolved so the beaks can be extracted easily. With large buccal masses one or two changes of solution may be necessary to complete the process.
   b. Potassium hydroxide. Potassium hydroxide is a strong base. The whole buccal mass is placed into a 3-5% (weight/volume) solution of KOH and boiled for 20-30 minutes. Tissues will then fall off the beaks or can be pulled

off. Beaks are then washed in running tap water for 2-3 hours. This method works well on large octopus buccal masses and beaks but is too traumatic for the more delicate squid beaks and larval or juvenile octopuses. These should be boiled for only 5-10 minutes or placed in a 5-8% (weight/volume) KOH solution for 12-24 hours without heating. Extracted beaks are washed thoroughly in running tap water for 2 hours (techniques of M. Nixon, 1969 and pers. comm.). Note—care must be taken when working with heated KOH and adequate protective clothing and goggles should be worn.

c. Sodium hydroxide. Sodium hydroxide, also a strong base, provides a much safer medium for beak extraction because it does not have to be heated or boiled. The buccal mass is placed in a 10% (weight/volume) solution of NaOH at room temperature for up to 24 hours. Frequent checking is recommended so that beaks can be extracted as soon as possible to avoid damage by the chemical. Wash the extracted beaks as noted above.

d. Chlorox. Chlorox (hypochlorite) will mascerate buccal mass muscles, especially from small specimens. The small buccal mass is placed in full strength chlorox for a few seconds then removed to fresh water to inspect the progress of masceration. Several immersions may be necessary depending on the size and consistency of the buccal mass. A less traumatic extraction can be achieved by using a dilute solution of chlorox; dilutions and durations should be determined experimentally. Extracted beaks should be thoroughly washed.

Beaks are preserved in the same alcohol preservatives as the specimens from which they are extracted. They should be returned to the specimen jar in a small, sponge-stoppered vial (each vial should be labelled if beaks from more than one specimen per lot are present). Drying is not recommended, as the desiccated chitin becomes very brittle and strongly distorted. Dried beaks can be protected from further breakage in a solution of 25% glycerine and 75% alcohol.

IV.D. *Radula*. The radula is extracted using the same techniques as applied to beaks. Once the beaks have been removed from the buccal mass the radula can be removed by gently pulling with forceps; occasional teasing or careful dissection might be necessary to loosen the radula from especially hardened masses. Wash the radula thoroughly in distilled water. Radulae can be examined temporarily on a glass slide with a cover slip. Preservation is the same as for beaks—the radula is placed in a vial, preferably with the beaks, and returned to the jar in which the animal is preserved. Permanent preservation also can be accomplished on slides as it is with other molluscan radulae. The cephalopod radula can be stored in 70% ETOH prior to mounting for optical microscopy. If it is to be examined by scanning electron microscopy (SEM) it must be run through a graded series of alcohols (70%, 85%, 100%) to dehydrate it and prevent shrinkage when it is dried. For optical microscopy, place the radula in a small amount of stained mounting medium (e.g., Turtox CMCP-9) until it is sufficiently stained. Then place unstained mounting medium (e.g., Turtox CMCP-10) on the final glass slide (flat or depression, depending on size of radula) and transfer the stained radula into it. It may be desirable to break the radula in several places with micro dissecting needles to allow easier examination of the teeth. Cover immediately with a cover slip and allow to set at least 12 hours; ring cover slip with clear nail polish, and label the slide with sufficient information to ensure its identity. Sealed slides can be stored in standard slide drawers or boxes.

To mount a radula for SEM examination, it should be carefully cleaned in an ultrasonic cleaner, then transferred from the absolute alcohol to a glass slide for orientation and drying (it may be necessary to break the radula). Remove the completely dried radula to a carefully cleaned SEM stub and mount with white glue (e.g., Elmer's) diluted 2:1 with

distilled water. Proceed with coating technique. (Above techniques courtesy of C. Hickman, pers. comm.)

IV.E. *Statoliths*. While the statoliths of cephalopods have not been extensively studied (with the exception of Ishikawa, 1924, 1929), a rapidly growing interest in them centres around their potential use in ageing studies. Also, statoliths seem to be specific enough in some groups to allow identification to the generic level which would be very helpful in fossil and stomach content studies (Clarke, 1978; Clarke & Fitch, 1979; Clarke *et al.*, 1980). Statoliths are small (usually less than 2 mm in length) calcareous stones composed of aragonite, and, as such, are very susceptible to dissolution in fixatives and preservatives that are in the least degree acidic. Consequently, they rarely are found in preserved specimens. Clarke (1978) gives the technique for extraction from fresh, unpreserved specimens which is summarized here. The funnel is removed, the head is flexed dorsoposteriorly, then the skin and the cartilage are sliced horizontally near the midline of the cranium between the posterior ends of the eyes until the statocysts are penetrated. The statoliths lie in the anterior end of the statocysts as small opaque to white stones. They should be removed with a micro probe, featherweight forceps, or microspatula. Normal forceps, even lightly squeezed, may crush them.

Statoliths can be preserved in small ampules or vials in buffered alcohol, mounted and sealed on slides, or desiccated and placed in covered depression slides.

IV.F. *Dehydrated specimens*. Specimens that have become hardened and dried through evaporation of preservative and subsequent dehydration may be partially rehydrated with one of the following solutions:

1. A solution of glycerine (glycerol) and ethanol is most effective on specimens that have not been completely desiccated and hardened. Begin with a ratio of 1 part glycerine by volume to 3 parts 75% ETOH, but experimentation with ratios might be necessary.
2. Tribasic sodium phosphate ($Na_3PO_4 \cdot 12H_2O$) in a 0.1% aqueous solution for 24 hours or longer has been effective on small specimens (larvae, juveniles).
3. Commercial wetting agent. We have had the greatest success with rehydration of desiccated specimens using the commercial wetting agent Areosol O.T. Solution, 10% aqueous (Fischer Scientific Company, Fair Lawn, New Jersey, USA. (Product endorsement is not implied by use of trade name or company name)).
4. Alconox or household detergents in strong concentrations in water are wetting agents that are useful as rehydration solutions.

Specimens should be kept in the rehydration solution, or in successive changes, until no additional improvement in the condition is noted (up to several weeks or months in the most severe cases). We emphasize that experimentation with concentrations of the solution and duration of exposure is encouraged, as no specific protocols have been established. Most dehydrated desiccated specimens never will regain their earlier state of preservation, but rehydration does improve material so that it can be worked with to some degree. Once rehydration is accomplished, specimens are preserved in the standard manner. Addition of glycerine (glycol) or propylene glycol to a 1-2% solution with the alcohol will help retain softness and pliability.

V. **Acknowledgements**

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GUIDELINES FOR TAXONOMIC DESCRIPTIONS OF CEPHALOPOD SPECIES

CONTENTS

GUIDELINES FOR TAXONOMIC DESCRIPTIONS OF CEPHALOPOD SPECIES

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Abstract

This paper presents a format of guidelines considered necessary for the description (or redescription) of species of cephalopods. These guidelines or standards include specific requirements for descriptive characters of species within the Orders Sepioidea, Teuthoidea and Octopoda as well as general information, e.g., synonymy, locality, etc. Standards are given for descriptions, counts of measurements, and illustrations. Appendices list definitions of counts, measurements, and indices; diagramatically illustrate standard measurements; and give examples from the literature of descriptions that approach these standards.

General Standards

Introduction. The need for minimum standards for the description of species in cephalopod systematics was addressed at the International Workshop on the Biology and Resource Potential of Cephalopods (Roper, 1983) sponsored by the National Museum of Victoria and the Victorian Institute of Marine Sciences and held at the Marine Sciences Laboratory, Queenscliff, Australia, 9-13 March 1981. We are most grateful to a number of the workshop participants who responded to the suggestion that the outline of the proposed standards be begun at the workshop. The discussion that ensued resulted in a significant percentage of the required and secondary characters being listed. So, to that important extent, these standards result from the combined efforts of these colleagues: S.v. Boletzky, R. Hanlon, F. G. Hochberg, C. C. Lu, T. Okutani, and R. E. Young. The authors also wish to thank Michael J. Sweeney for his valuable contribution in compiling notes, verifying and expanding the characters and definitions based on searches in the literature, and overall assistance in preparing the manuscript. The illustrations were prepared by Carolyn Gast, to whom appreciation is expressed. Valuable comments on the manuscript were received from F. M. Bayer, S. D. Cairns, and F. G. Hochberg.

At the outset it is important to point out that international standards exist for the naming of new zoological species (and other taxa). The naming of any new taxon should adhere to the rules and recommendations of the International Code of Zoological Nomenclature (Stoll *et al.*, 1964).

The following criteria are considered necessary to adequately describe a new species or to redescribe a species inadequately described originally. Ideally, at least five specimens consisting of both males and females should be considered as a prerequisite for describing a new species. Greater numbers, however, are strongly preferred in order to present an indication of the range of variability in various characters with respect to size (age), sex and geographic distribution. It is recognized, of course, that some new species may be represented by fewer than five specimens. While it is advisable to have additional material, unusual circumstances (unquestioned distinctiveness of the species, the high probability that no additional material will be forthcoming soon) may make it necessary to describe the species. This should be done only in very well justified cases. In any new description, all measurements, counts and indices used must adhere to standard definitions or be completely defined in order to facilitate direct comparison with descriptions of other species. Appendix 1 presents a list of definitions for the most commonly used meristic characters. This is based on the definitions given by Voss (1963) but is modified and expanded to reflect changes and

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increases in knowledge since that time. Appendix 2 contains diagrammatic illustrations of the more frequently used measurements.

Definition. The family and genus into which the species is placed should be defined based on recognized definitions cited from the literature, or they should be redefined. Clear justification must be made for placing the species in a genus; the species must be clearly differentiated from all other species in that genus. If related genera are not well defined, or if their criteria are questionable, the new species should be clearly differentiated from all species in the related genera, as well. The unique or diagnostic features of the new species should be pinpointed. Appendix 3 cites papers which contain examples of adequately described taxa.

Synonymy. The synonymy in essence is a summary of the nomenclatural history of a specific entity. If the information presented is either a description of a new species or a redescription of a previously named species, a synonymy giving specific citations should be included. The synonymy serves as an additional source of information as well as a list of identified specimens other than those in the Material Examined section. The synonymy should distinguish between works that describe a single species under more than one taxonomic name and one taxonomic name containing specimens of more than one species.

Material Examined. This section of the species description should list all specimens examined by the author. The HOLOTYPE always should be the first specimen listed, followed by any other designated type-material (PARATYPE(S)). The remainder of the specimens examined follows, designated as "other material" or "additional material". Some of the other material could be specimens examined by the author that are listed in the synonymy section from previously published papers. Data for holotype and paratypes must be presented separately for each specimen: sex, ML, etc. Data for all other specimens examined should be presented in the following order: number of specimens (if several are from the identical specimen lot) and sexes, mantle length(s) (minimum and maximum, by sex), collector (e.g., individual, ship) and station number, locality by place name and latitude and longitude, depth collected, collecting gear or technique, date collected, and museum catalog number. The last element of data, the MUSEUM CATALOG NUMBER, is strongly emphasized as it permits rapid location in the future of individual specimen lots in collections and of additional information.

Description. Details are given below under each order; also, see Definitions of Characters.

Type Designation. A description of a new species and a redescription of a species with an extant holotype should list the type-specimen (HOLOTYPE), the museum where it is deposited and the museum catalog number for that specimen. If a NEOTYPE or LECTOTYPE is designated in the process of a redescription, it is listed in the same manner as a HOLOTYPE. All type-specimens must be specifically labelled as HOLOTYPE, PARATYPE, LECTOTYPE, etc.

Type-Locality. The geographic locality of the primary type and other pertinent data are presented here for quick reference. A general description of the area (i.e., North Atlantic Ocean, off Galapagos Islands, Australia, Southern Ocean, etc.) and the specific latitude and longitude of the collecting point are required. The depth of capture and other pertinent data should also be given.

Distribution and Habitat. The limits of the known geographic distribution and areas of concentration of the species should be defined in this section. Areas of apparent absence should be analysed in view of sampling limitations. The range of vertical distribution also should be determined using both discrete (e.g., closing-net, on-site, bottom gear) and non-discrete (e.g., non-closing midwater trawls, deep benthic trawls, etc.) depth records. Habitat information should be presented, as well, if available (e.g., bottom type, habitat type, water mass type).

Discussion. Detailed comparisons with other species in the genus are of prime importance in this section. Comparisons should include key characters and address specific similarities and differences. Proper comparisons may necessitate the detailed examination, or even redescription, of related species, if they are in-

sufficiently known. Differences in locality, size, etc. should be noted, but they are not sufficient in themselves to distinguish species. The actual morphological characters must be compared and contrasted. Frequently, graphs and tables are useful for this purpose.

Definitions of Characters. The definitions consist of a compilation from several relatively recent systematic works as well as some terms newly formulated for completeness. Also, some of the definitions may be slightly altered from their original form in earlier publications because of increased knowledge about the character or of a possibility for a more broadly applicable definition. Note that all measurements or counts on arms, tentacles and clubs customarily are made on the right-side appendages (or both right and left); if a right-side appendage is damaged or missing, the left-side one may be used, and designated as such. Also note that for each measurement it is possible to calculate an index as a method of comparison against a standard. Usually the standard is mantle length, but occasionally it may be another morphological feature of which the measured character is a part (e.g., gladius width index has the gladius length as the standard).

It is important to point out that not all definitions herein will apply equally well to a specific feature in all species. Because of the possibility (probability) of variation in an atypical taxon, an author is encouraged to define very carefully any deviations from these standards. Also, of course, not all counts, measurements and indices listed here can be applied to each species of cephalopod, i.e., some are specific to octopods, or squids, or cuttlefishes. Furthermore, a new species may have a meristic character not included in this list. If so, that particular character count, measurement, or index must be carefully defined consistent with the standard definitions.

Frequently in the past, authors have presented only raw data, that is, only the measurements of characters. Because indices represent a refinement of raw data against a standard, they permit comparisons of differences caused by growth. The use of indices allows comparisons within a population (collection) of a single species as well as between populations of two or more species. Thus indices have become a very useful tool in descriptive systematics of cephalopods. It is here very strongly urged that authors of new species or of redescriptions include the indices in addition to the raw data. Also, whenever indices are used (e.g., in tables, graphs, etc.) the mantle length(s), the standard of size in all cephalopods, must be listed. Because the indices are so important and their use is so strongly encouraged, the definitions of measurable characters presented in Appendix 1 are of the indices rather than the raw measurements. However, the definition of the actual measurement is inherent in the definition of the index; therefore, no confusion should arise should an author wish to use a raw measurement definition.

Additional comments concerning data not covered in other sections are helpful: e.g., behaviour, non-permanent color patterns observed on live specimens, bottom or habitat preference, abundance, prey, predators, etc. Since parasites frequently are host-specific, they should be described and identified to lowest possible taxon; the aid of a specialist is recommended.

The *etymology* of the new name is highly recommended, and the name must conform to the requirements of the International Code of Zoological Nomenclature (Stoll *et al.*, 1964).

Ordinal Standards

The different groups ("orders") of cephalopods have somewhat different descriptive requirements because of their different morphologies and characteristics. The three major groups—cuttlefishes, squids, and octopuses—each are discused separately under sections on description, counts and measurements, and illustrations.

The written description is the most important part of the analysis of a species description. Every effort must be made to choose carefully the words for an accurate, clear, concise species description. The anatomical features listed below for each group must be carefully described to achieve a complete and accurate description. Clearly this paper cannot list every character or variation or modification of

characters that exists for any given species. Nor will each species necessarily possess all characters listed. Every author is responsible for insuring that each character is thoroughly scrutinized and described, regardless of whether that character is listed herein.

A. ORDER SEPIOIDEA—SEPIIDAE (CUTTLEFISHES), SEPIOLIDAE, ETC.

Description. The following characters are to be included in the description of a new species of Sepioidea:

1. Mantle: shape, thickness, musculature, width, sculpture, pigmentation patterns
2. Cuttlebone (Sepion): shape, sculpture, striations, spine, coloration
3. Gladius (in non-cuttlefish): shape, sculpture, thickness, width, and length of rachis, vane, and conus
4. Arms: arm formula (by decreasing length), number and spacing of longitudinal rows of suckers (basal, medial and distal sections), swimming keel(s), dorsal and ventral protective membranes and trabeculae, attenuation of tips
5. Hectocotylus: arm(s) involved, arrangement of suckers, loss, enlargement, reduction or other modification of suckers, modification of sucker stalks, protective membranes and trabeculae, presence of pits, ridges, or papillae
6. Club and Tentacle: dorsal and ventral protective membranes and whether they are united or separate at base of club; trabeculae; arrangement, size and number of rows of suckers in each section (carpus, manus, dactylus); shape and size (e.g. robustness) of club and tentacular stalk; swimming keel(s); clefts
7. Suckers (arms and clubs): shape, absolute and comparative sizes, dentition of rings, soft rings
8. Buccal Mass: membrane, lappets, connectives, suckers
9. Spermatophore Pad: location, shape, and structure in females
10. Beak: shape, pigmentation, angles, etc. of component parts; several sizes and sexes—(See Clarke, in prep.)
11. Radula: number, shape and relative size of teeth in a transverse, unused row; cusps; lateral plates. (Check several specimens for variation)
12. Reproductive system: all male and female component parts
13. Spermatophores and Eggs: shape, size, number, component parts of spermatophores
14. Integumentary features: permanent color patterns, chromatophores, sculpture, papillation, supplement with observations of live animal if possible
15. Fins: shape, extent, width, attachment
16. Digestive tract: nature of digestive gland, pancreatic tissue, ducts, spiral caecum, stomach, crop, intestine, anus
17. Funnel Organ: shape, sculpture, dorsal and ventral components
18. Funnel-mantle Locking Cartilage: mantle and funnel components, shape, size
19. Photophores: location, type, shape, size, number
20. Parasites (often host-specific): identify group and lowest possible taxon; seek aid of specialist.

Counts and Measurements. Counts and measurements in millimetres (mm) (or centimetres (cm) for large species) for sepioids should be presented in a table for the structures listed below. These counts and measurements are a minimum for the description; those given in brackets also should be included for completeness but may not be critical. Most measurements can be given as an index, a direct proportional relationship to the mantle length, the standard length of all cephalopods. The index is determined by the formula:

$$\frac{\text{Character Measurement}}{\text{ML}} \times 100 = \text{Index}$$

$$\text{e.g., ML}=270\text{ mm, HW}=33\text{ mm: } \frac{33}{270} \times 100 = 12.2$$

Direct measurements of all characters may appear in the table with indices or in an appendix, if desired. See Appendix 1 for standard definitions and Figure 1. Because some characters are so different between groups, a standard defini-

tion may not apply; in these cases the modified definition is given with the character.

1. Mantle Length (ML); [Total length (TL), Ventral Mantle Length (VML) – use VML only when significant differences exist between dorsal and ventral lengths, as in *Stoloteuthis* or *Nectoteuthis*]
2. Mantle Width Index (MWI) – greatest straight-line width across ventral surface of mantle (excluding fins) as a percentage of mantle length
3. Fin Length Index (FLI)
4. Fin Width Index (FWI)
5. Head Width Index (HWI); [Head Length Index (HLI)]
6. Arm Length Index (ALI); [Arm Formula (AF)]
7. Arm Sucker Index (ASIn for normal, ASIe for enlarged); [Arm Sucker Count (ASC), Sucker Teeth Count (STC)]
8. Club Length Index (ClLI)
9. Club Row Count (ClRC)
10. Club Sucker Index (ClSI)
11. Hectocotylus Length Index (HcLI); [Hectocotylized Arm Index (HcAI)]
12. Spermatophore Length Index (SpLI); [Spermatophore Width Index (SpWI)]
13. Egg Length Index (EgLI)
14. Gill Lamellae Count (GiLC)
15. Cuttlebone Length (CbL)
16. Striated Zone Index (StZI)
17. Cuttlebone Width Index (CbWI)
18. [Eye Diameter Index (EDI), Lens Diameter Index (LnDI)]

Illustrations. Illustrations of the following characters are highly recommended in support of the descriptive section for sepioids. Those designated by an asterisk are especially important. Always include the mantle length of the specimen from which the illustrated character was drawn and the size of the scale unit.

1. Whole animal, dorsal* and ventral view
2. Funnel organ*
3. Funnel-mantle locking cartilage*
4. Club*, including suckers, membranes, keels, clefts
5. Sucker rings*, club and arms
6. Hectocotylized arm(s)*
7. Beak and radula
8. Reproductive system, male and female
9. Spermatophores and eggs
10. Cuttlebone*, dorsal and ventral views; inner and outer cone, amount of fusion; spine; lateral wings; dorsal and/or ventral keels on spine
11. Stellate ganglion
12. Color photograph of living animal, if possible (to be deposited with holotype)
13. Oral view*, all arms spread out (divide between arms IV) in both sexes (very important for sepiolids)
14. Photophores* – if present
15. Gladius* – if present (in some sepiolids), whole and series of cross section, in detail, not diagrammatic.

B. ORDER TEUTHOIDEA – NERITIC AND OCEANIC SQUIDS

Description. The following characters are to be included in the description of a new species of teuthoid squid:

1. Mantle: shape, thickness, musculature, width, sculpture
2. Gladius: shape, sculpture, thickness, width, and length of rachis, vane, and conus
3. Fins: shape, margins, extent, attachment, tail
4. Funnel: shape, extent, musculature, funnel valve, funnel organ
5. Funnel-Mantle Locking Cartilage: type, shape, size, sculpture
6. Head: shape, eyes, eyelids, olfactory papillae, nuchal folds, nuchal locking-cartilage
7. Arms: arm length in decreasing order (= formula); number of longitudinal sucker and/or hook rows; suckers, sucker rings (chitinous and soft), hooks; keels, membranes, trabeculae, papillation; attenuation, robustness
8. Hectocotylus: arm(s) modified; sucker arrangement, loss or reduction; pits, holes, ridges, papillae, membranes, trabeculae, attenuation

9. Spermatophore Pad or Receptacle (on female): shape, location, sculpture
10. Tentacle and Club: tentacle—stalk-size, length, cross-section, suckers on stalk; club—carpus, manus and dactylus, number of sucker rows (transverse and longitudinal), suckers, sucker rings, hooks, knobs, keels, membranes, papillation, trabeculae, size, attenuation
11. Buccal Mass: membrane, lappets, connectives, suckers
12. Beak: shape, pigmentation, angles, etc.; several sizes and sexes—(See Clarke, in prep.)
13. Radula: number, relative size, and shape of teeth in a transverse, unused row; cusps; lateral plates (Check several specimens for variation)
14. Chromatophores: location, color, patterns, densities; suppliment with observations of live animal
15. Photophores (Light Organs): location, type, shape, size, number; internal, external
16. Spermatophores: shape, size, details of component parts; number
17. Eggs: shape, size, number
18. Reproductive System: component parts of mature male and female
19. "Larval stages": if different from adult
20. Parasites (often host-specific): identify group and lowest possible taxon; seek aid of specialist

Counts and Measurements. Counts and measurements in millimetres (mm) (centimetres (cm) acceptable for very large species) for squids should be presented in a table for the structures listed below. These counts and measurements are a minimum for the description; those that follow in brackets should be included for completeness. Refer to Sepioid section for details on determining indices. See Appendix 1 for standard definitions, and Figures 2 and 3.

1. Mantle Length (ML); [Total Length (TL)]
2. Mantle Width Index (MWI)
3. Gladius Length (GL); [Gladius Length Index (GLI), Gladius Width Index (GWI), Rachis Length Index (RLI), Rachis Width Index (RWI)]—see Toll, 1982
4. Fin Length Index (FLI)
5. Fin Width Index (FWI)
6. Arm Length Index (ALI); [Arm Formula (AF), Arm Hook Count (AHC), Arm Sucker Count (ASC), Arm Sucker Index (ASIn and ASIe)
7. Club Length Index (ClLI); [Club Sucker Index (ClSI)]
8. Club Row Count (ClRC); [Carpal Sucker Count (CSC), Dactylus Sucker Count (DSC), Manus Sucker Count (MaSC), Manus Hook Count (MaHC), Transverse Row Count (TrRC)]
9. Hectocotylus Length Index (HcLI); [Hectocotylized Arm Index (HcAI)]
10. Sucker Teeth Count (STC)—for largest suckers on manus, dactylus, arm III and arm IV, especially
11. Head Length Index (HLI)
12. Head Width Index (HWI)
13. Lens Diameter Index (LnDI); [Eye Diameter Index (EDI)]
14. Lappet Sucker Count (LpSC)
15. Spermatophore Length Index (SpLI)
16. Sperm Reservoir Index (SpRI)
17. Spermatophore Width Index (SpWI)
18. Gill Lamellae Count (GiLC)
19. [Egg Length Index (EgLI), Tentacle Length Index (TtLI), Tubercular Ridge Index (TbRI)]

Illustrations. Illustrations of the following characters are highly recommended in support of the description of squids. They should be as detailed as possible and consistent with the description. Always include the mantle length of the specimen from which the illustrated character was drawn and the size of the scale unit.

1. Whole animal, dorsal* and ventral view
2. Funnel organ*
3. Funnel-mantle locking cartilage*, both components
4. Tentacular club* and tentacular stalk (if bearing armature), including armature, keels, membranes, etc.
5. Hectocotylus*

6. Largest sucker (with stalk), or a series*, from arms III and IV (at least) and from manus and dactylus (both inner and outer chitinous rings should be visible, or make 2 drawings if necessary.) (Scanning electron micrographs are an excellent substitute for illustrations of sucker dentition.)
7. Photophores* and their distribution (very important for many teuthoid species)
8. Beak and radula*
9. Gladius*, whole and series of cross-sections
10. Largest hook from tentacular club and arms III and IV; or a series
11. Larval stages, if morphologically different from the adult
12. Reproductive system, male and female
13. Spermatophore and eggs

C. ORDER OCTOPODA—BENTHIC AND PELAGIC OCTOPUSES

Description. Octopods are subject to changes in morphology due to preservation to a much more pronounced degree than either cuttlefishes or squids. For this reason it is very important that the preserved specimens used for the description are typical of the species as a whole. Live or recently dead specimens should be examined and measured for comparison whenever possible.

Because some benthic octopods have the ability to elongate their mantles and contract back to normal (e.g., *Octopus ornatus*), measurements using mantle length as a standard can be greatly affected. In such cases the author should indicate that the mantle is elongated and thus has distorted the indices (see Voss, 1981 re *O. ornatus*). The normal range of changes in octopods may or may not affect the range of means of indices. In the cirroteuthids, the mantle musculature is very weak and a significant part of the mantle length lies posterior to the shell vestige. This portion is subject of great shrinkage in preservation and in many genera (*Stauroteuthis*, *Cirroteuthis*, etc.) makes indices using mantle length nearly meaningless. Good judgement has to be exercised and several workers have found the interocular width to be less distorted and have used that measurement as a standard. Whichever character is used, it must be clearly stated. Workers are urged to remain aware of these problems and to deal with them on a species-by-species basis.

The anatomical features listed below must be carefully described to achieve a complete and accurate species description.

1. Mantle: shape, thickness; mantle opening
2. Head: shape; eyes, dimensions
3. Funnel: shape, size; funnel opening; funnel organ
4. Arms: arm formula; robustness, attenuation; number of sucker rows, cirri
5. Suckers: number; absolute and comparative sizes; patterns, sculpture; presence and position of enlarged suckers
6. Web: formula; thickness; extent or depth; extension out the side(s) of the arms (state which side)
7. Hectotylus: location (arm number, right or left side), shape, size; ligula, calamus, membrane, sculpture
8. Gills: shape, number of lamellae on each demibranch; example, 9 outer 7 inner
9. Digestive tract: shape, size (salivary glands, crop, stomach, spiral caecum, digestive gland, anus, ink sac); extent of involvement of ink sac in digestive gland (surface, buried or absent)
10. Reproductive system: shape, size (details of all male and female components)
11. Spermatophores and eggs: configurations; sizes, egg maturity (with or without striations)
12. Beak: shape, pigmentation, angles; several sizes and sexes—(see Clarke, in prep.)
13. Radula: number; relative size, and shape of teeth in a transverse unused row; formula (Check several specimens for variation)
14. Integumentary features: permanent color markings or patterns, chromatophores, ocellae, white patches, sculpture, papillae, rugosity, supple-

ment with observations of live animals if possible

15. Stellate ganglion: configuration; size of fin nerves
16. Eyes: size
17. Live animal characteristics: habitat, behavior
18. Larvae: if planktonic, presence of Kolliker's bristles
19. Parasites (often host-specific): identify group and lowest possible taxon; seek aid of specialist
20. Shell vestage (fin cartilage): shape, cross-section; for both sexes (cirrates)
21. Olfactory organ: presence, size, shape (cirrates)
22. Optic lobe and "White body": length, width (especially cirrates); types of nerves and bundles
23. Fins: shape, size (cirrates)

Counts and Measurements. Counts and measurements for the octopod structures listed below should be presented in a table. These counts and measurements are considered a minimum for the description; those that follow in brackets should be included for completeness. Refer to sepioid section for details on determining indices. See Appendix 1 for standard definitions and Figure 4.

1. Mantle Length (ML)
2. Mantle Width Index (MWI)
3. Head Width Index (HWI); [Head Length Index (HdLI)]
4. Mantle Arm Index (MAI)
5. Arm Length Index (ALI); [Arm Formula (AF)]
6. Arm Width Index (AWI)
7. Arm Sucker Count (ASC)
8. Arm Sucker Index (ASIn and ASIe).
9. Web Depth Index (WDI); [Web Formula (WF)]
10. Hectocotylus Length Index (HcLI)
11. Opposite Arm Index (OAI); [Hectoctylized Arm Index (HcAI)]
12. Ligula Length Index (LLI)
13. Calamus Length Index (CaLI)
14. Gill Lamellae Count (GiLC)
15. Total Length (TL)
16. Spermatophore Length Index (SpLI); [Spermatophore Width Index (SpWI), Penis Length Index (PLI), Penis Diverticulum Length Index (PdLI)]
17. Egg Length Index (EgLI)
18. Cirrus Length Index (ClLI)
19. Funnel Length Index (FuLI)
20. Free Funnel Index (FFuI)
21. Pallial Aperature Index (PAI)
22. [Eye Diameter Index (EDI), Eye Orifice Index (EOI), Lens Diameter Index (LnDI)]

Illustrations. The following illustrations are strongly recommended in support of the descriptive section for octopods. Always include the mantle length of the specimen from which the illustrated character was drawn and the size of scale unit.

1. Whole animal, dorsal* view; color pattern, ocellae, papillation
2. Lateral and/or ventral view of animal if permanent color pattern or papillation dictates
3. Ventral view of mantle opening and funnel*
4. Funnel organ*
5. Oral view* of portion of arm with unusually enlarged suckers or with cirri
6. Hectocotylus*—entire and details of calamus and ligula
7. Beak and radula
8. Viscera—ventral view of arrangement of organs in mantle cavity
9. Digestive tract*—dissected out
10. Male and female genitalia*—dissected out
11. Spermatophores* and eggs
12. Stellate ganglion*
13. Color pattern(s)*, ocellae* (drawn from live animal, if possible) and papillation (supplement with color photographs)
14. Oral view* of arms, cirri, primary and secondary webs of cirrates
15. Fin cartilage* of cirrates (both sexes)
16. Optic lobe and White body
17. Olfactory organ of cirrates

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Appendix 1. Definitions of counts, measurements (in mm), and indices of cephalopods.

Refer to the discussion section (p. 51) of the text before applying these definitions, as certain qualifications must be understood.

Arm Formula—AF: comparative length of arms expressed numerically in decreasing order, e.g., 3.4.2.1., 3.2.4 = 1. or III.IV.II.I. etc.

Arm Length Index—ALI: length of arm measured from first basal (proximal-most) sucker to tip of arm in squids and cuttlefishes as a percentage of mantle length; measured from beak to tip of arm in octopods. (Arm I, dorsal; II, dorso-lateral; III, ventro-lateral; IV, ventral).

Arm Hook Count—AHC: number of hooks on basal (proximal) half of each designated arm.

Arm Sucker Count—ASC: number of suckers on basal half of each designated arm.

Arm Sucker Index—ASIn: diameter of largest normal arm sucker on each designated arm as a percentage of mantle length. ASIe: diameter of largest enlarged arm sucker (state which arm) as a percentage of mantle length. (See illustration in Appendix 2).

Arm Width Index—AWI: width of stoutest (right) arm at mid-point of arm length as a percentage of mantle length (measurement exclusive of webs and membranes).

Calamus Length Index—CaLI: in octopods, length of calamus measured from last (distal-most) sucker to its distal tip as a percentage of ligula length. Warning—a better measurement needs a definite starting point.

Carpal Sucker Count—CSC: number of suckers and knobs on carpus of (right) club, e.g., 7 suckers, 6 knobs.

Cirrus Length Index—CiLI: length of longest cirrus on each arm as a percentage of the diameter of the largest normal sucker; (alternative: as a percentage of interocular width).

Club Length Index—ClLI: length of designated club as a percentage of mantle length. Club length is measured from proximal base of carpal cluster of proximal-most carpal sucker or knob to distal tip of club or, in those species having no distinct carpal cluster, from proximal-most basal sucker that truly is part of the club.

Club Row Count—ClRC: number of longitudinal rows of suckers and/or hooks across the width of the club. Define when used—rows may be counted as longitudinal (parallel with the long axis of the club) or oblique for dactylus or manus.

Club Sucker Index—ClSI: diameter of largest sucker on (right) club as a percentage of mantle length.

Cuttlebone Length—CbL: dorsal length of cuttlebone along midline, including spine.

Cuttlebone Width Index—CbWI: greatest width of cuttlebone as a percentage of cuttlebone length.

Dactylus Sucker Count—DSC: number of suckers on dactylus of (right) club.

Egg Length Index—EgLI: length of (mature) egg as a percentage of mantle length. (Eggs should be taken from the oviduct to ensure greatest degree of maturity, or preferably use spawned eggs if available.)

Egg Width Index—EgWI: greatest width of (mature) egg as a percentage of mantle length. (Eggs should be taken from the oviduct to ensure greatest degree of maturity, or preferably use spawned eggs if available.)

Eye Diameter Index—EDI: diameter of eye across bulbus as a percentage of mantle length.

Eye Orifice Index— EOI: diameter of the opening of the eye as a percentage of mantle length.

Fin Length Index—FLI: greatest length of fins as a percentage of mantle length. (May or may not include "tail".) (In cirrate octopods—length from midpoint of base of fin to the outer tip as a percentage of head width.)

Fin Width Index—FWI: greatest width (dorsally) across both fins as a percentage of mantle length. (In cirrate octopods—greatest width across one fin perpendicular to the fin length as a percentage of fin length.)

Funnel Length Index—FuLI: the length of the funnel from the anterior funnel opening to the posterior border measured along the ventral midline as a percentage of mantle length.

Free Funnel Index—FFuI: the length of the funnel from the anterior opening to the point of dorsal attachment to the head as a percentage of mantle length.

Gill Lamellae Count—GiLC: number of lamellae on outer demibranch, and inner demibranch including the terminal lamella(e); e.g., 9 outer, 7 inner.

Gladius Length—GL: dorsal length of gladius along midline.

Gladius Length Index—GLI: length of gladius as a percentage of mantle length.

Gladius Width Index—GWI: greatest width of gladius as a percentage of gladius length.

Head Length Index—HLI: dorsal length of head measured from point of fusion of dorsal arms to anterior tip of nuchal locking cartilage, or to some definable point if no nuchal locking cartilage exists.

Head Width Index—HWI: greatest width of head at level of eyes as a percentage of mantle length. (Same as interocular distance in octopods.)

Hectocotylized Arm Index—HcAI: length of hectocotylized arm measured from proximal-most armature, or

defined proximal point, to tip as a percentage of mantle length.

Hectocotylised Length Index—HcLI: length of modified portion of arm(s) measured from proximal-most modified sucker (or hook) to tip of arm as a percentage of total length of hectocotylized arm (define distal point if modification does not extend to arm tip).

Lappet Sucker Count—LpSC: total number of suckers on buccal lappets; may be given as number on individual lappets, then summed.

Lens Diameter Index—LnDI: diameter of eye lens as a percentage of mantle length.

Ligula Length Index—LLI: in octopods, length of ligula measured from distal-most sucker to tip of arm as a percentage of length of hectocotylized arm.

Mantle Arm Index—MAI: in octopods, mantle length as a percentage of longest arm.

Mantle Length—ML: dorsal mantle length. In decapods, measured from anterior most point of mantle to posterior apex of mantle or tip of united fins, whichever is longest. In octopods, measured from midpoint between eyes to posterior end of mantle.

Mantle Width Index—MWI: greatest straight-line (dorsal) width of mantle as a percentage of mantle length (ventral width is used in sepiids).

Manus Hook Count—MaHC: number of hooks on manus of (right) club.

Manus Sucker Count—MaSC: number of suckers on manus of (right) club.

Nuchal Commissure Index—NCI: width of nuchal commissure as a percentage of mantle length.

Opposite Arm Index—OAI: length of hectocotylized arm as a percentage of its fellow arm on opposite side (in octopods).

Pallial Aperture Index—PAI: the measurement between the points of attachment of the mantle to the head along the ventral margin of the mantle as a percentage of mantle length. (Same as mantle aperture index.)

Penis Length Index—PLI: in octopods, length of penis and diverticulum as a percentage of mantle length.

Penis Diverticulum Length Index—PdLI: length of penis diverticulum as a percentage of total penis length.

Rachis Length Index—RLI: length of free rachis measured from anterior end of gladius to point where anterior edge of vane joins rachis, as a percentage of gladius length.

Rachis Width Index—RWI: width of rachis measured at point where anterior edge of vane meets rachis as a percentage of gladius length.

Striated Zone Index—StZI: length of striated zone on ventral surface of cuttlebone as a percentage of cuttlebone length.

Sucker Diameter Index—SDI: the diameter measured across the aperture from outer rim to outer rim as a percentage of mantle length.

Sucker Teeth Count—STC: number of teeth on chitinous sucker rings.

Sperm Reservoir Index—SpRI: length of sperm reservoir as a percentage of total spermatophore length.

Spermatophore Length Index—SpLI: length of spermatophore as a percentage of mantle length.

Spermatophore Width Index—SpWI: greatest width of spermatophore as a percentage of spermatophore length.

Tentacle Length Index—TtLI: total length of tentacular stalk and club as a percentage of mantle length.

Total Length—TL: in decapods, measured from tip of club to posterior most point of mantle or tip of united fins, whichever is longest. In octopods, measured from end of longest arm to posterior end of mantle.

Transverse Row Count—TrRC: number of transverse (latitudinal) rows of suckers along the club or a portion of the club (e.g., entire club, manus, dactylus). Define proximal and distal points.

Tubercular Ridge Index—TbRI: length of tubercular ridge as a percentage of mantle length (in Cranchiidae, Histioteuthidae).

Ventral Mantle Length—VML: ventral mantle length measured from anterior border of mantle at ventral midline, to apex of mantle or tip of united fins, whichever is longest.

Web Depth Index—WDI: in octopods, measurement of deepest (most extensive) sector of web measured from mouth to midpoint of sector between arms as a percentage of longest arm. (Web sector A, dorsal to dorsal arm; B, dorsal to dorso-lateral; C, dorso-lateral to ventro-lateral; D, ventro-lateral to ventral; E, ventral to ventral.)

Web Formula—WF: comparative depth of each web sector measured from mouth to midpoint of sector between arms expressed alphabetically in decreasing order (e.g., B.C.D. = A.E., see Web Depth Index for sector definitions).

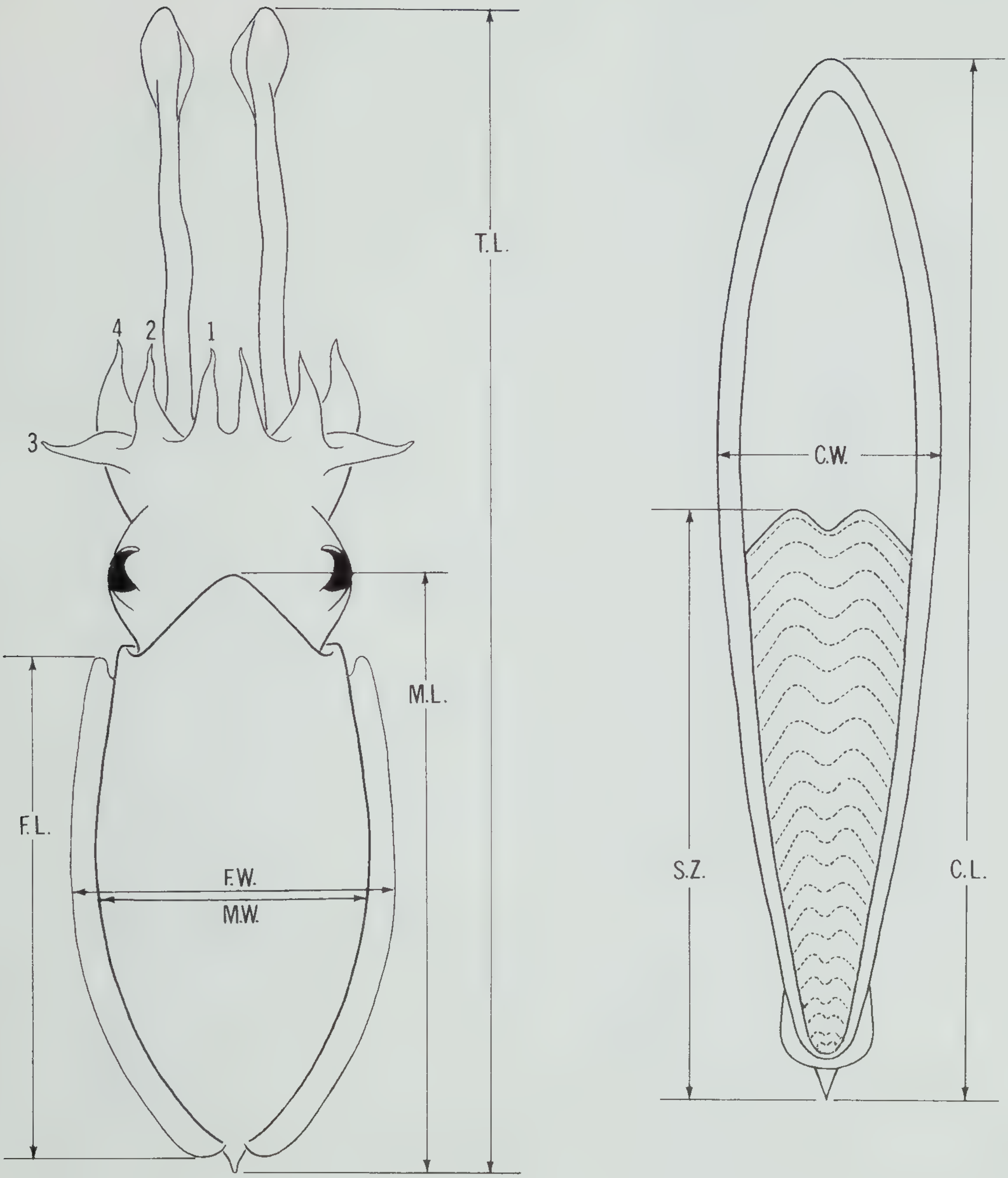
Appendix 2. Diagrammatic illustrations of frequently used measurements in cephalopods.

Figure 1. Sepioidea, Sepiidae. a. Dorsal view: FL = Fin Length, FW = Fin Width, ML = Mantle Length (dorsal), MW = Mantle Width, TL = Total Length. b. Cuttlebone, ventral view: CL = Cuttlebone Length, CW = Cuttlebone Width, SZ = Striated Zone.

Figure 2. Teuthoidea. a. Dorsal view, composite diagram. ED = Eye Diameter, FL = Fin Length, FW = Fin Width, HL = Head Length, HW = Head Width, ML = Mantle Length, MW = Mantle Width, TL = Total Length, TtL = Tentacle Length; Left eye = oegopsid eye, Right eye = myopsid eye. b. Gladius, ventral view. GL = Gladius Length, GW = Gladius Width, RL = Rachis Length, RW = Rachis Width.

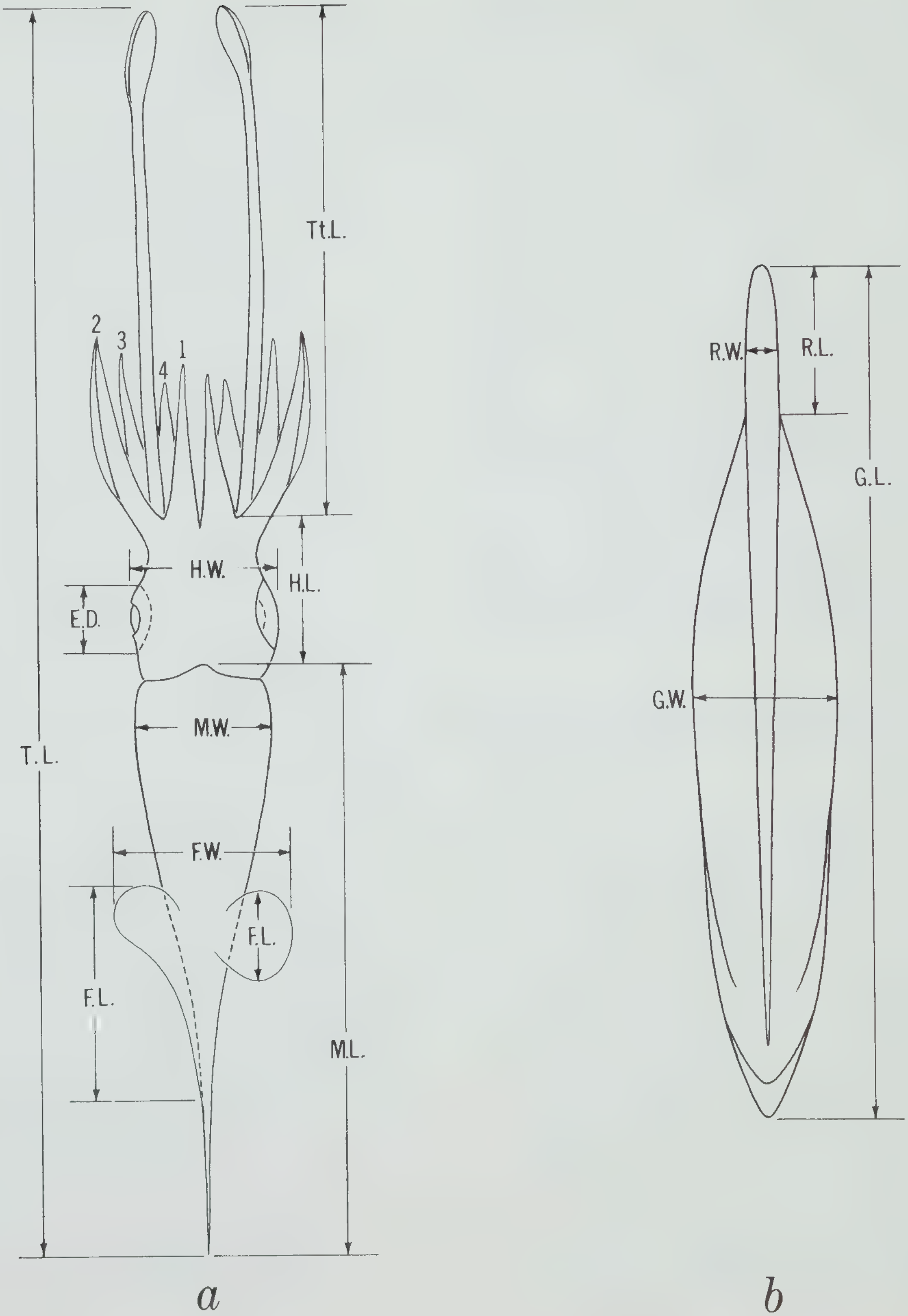
Figure 3. Teuthoidea. a. Hectocotylized Arm: AL = Arm Length, AW = Arm Width, HL = Hectocotylus Length. b. Tentacle and Club: CL = Club Length, CS = Club Sucker (largest), TtL = Tentacle Length.

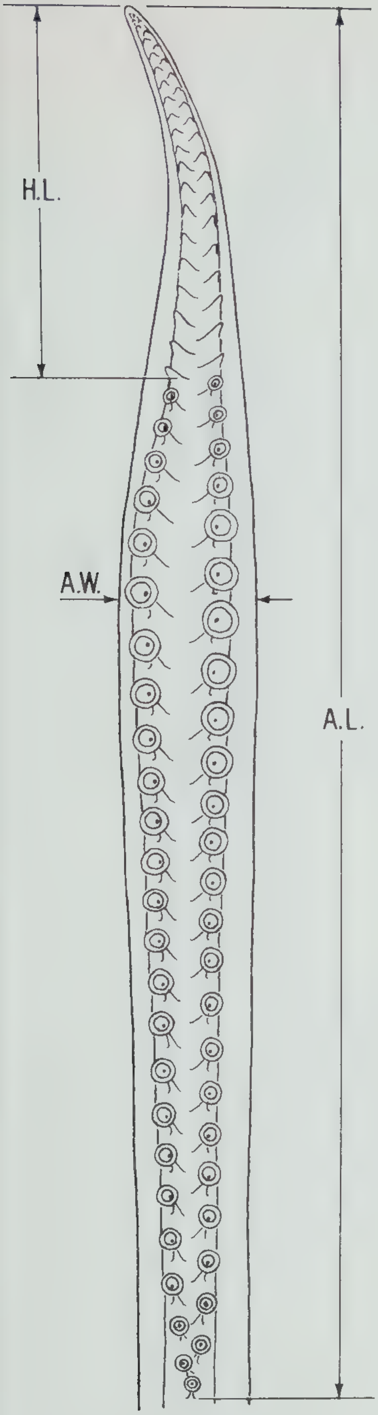
Figure 1



a *b*

Figure 2




H.L.
A.W.
A.L.
a

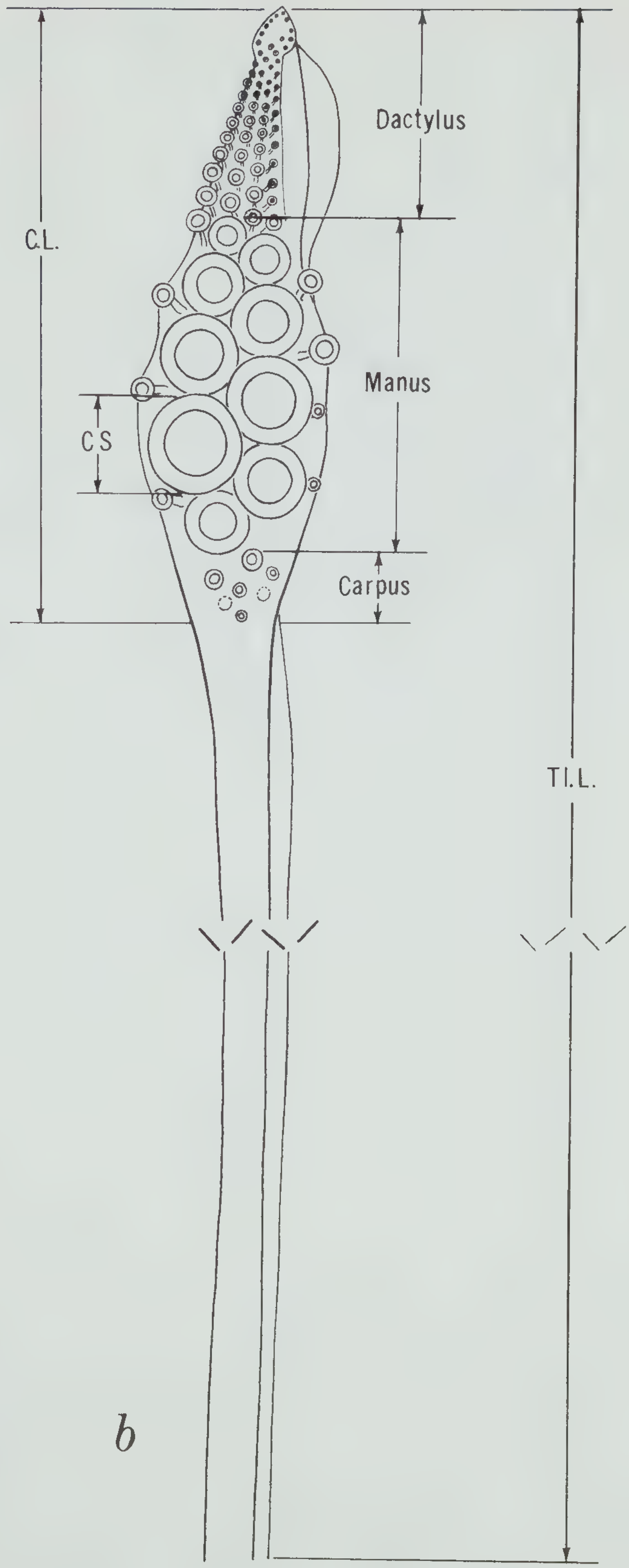
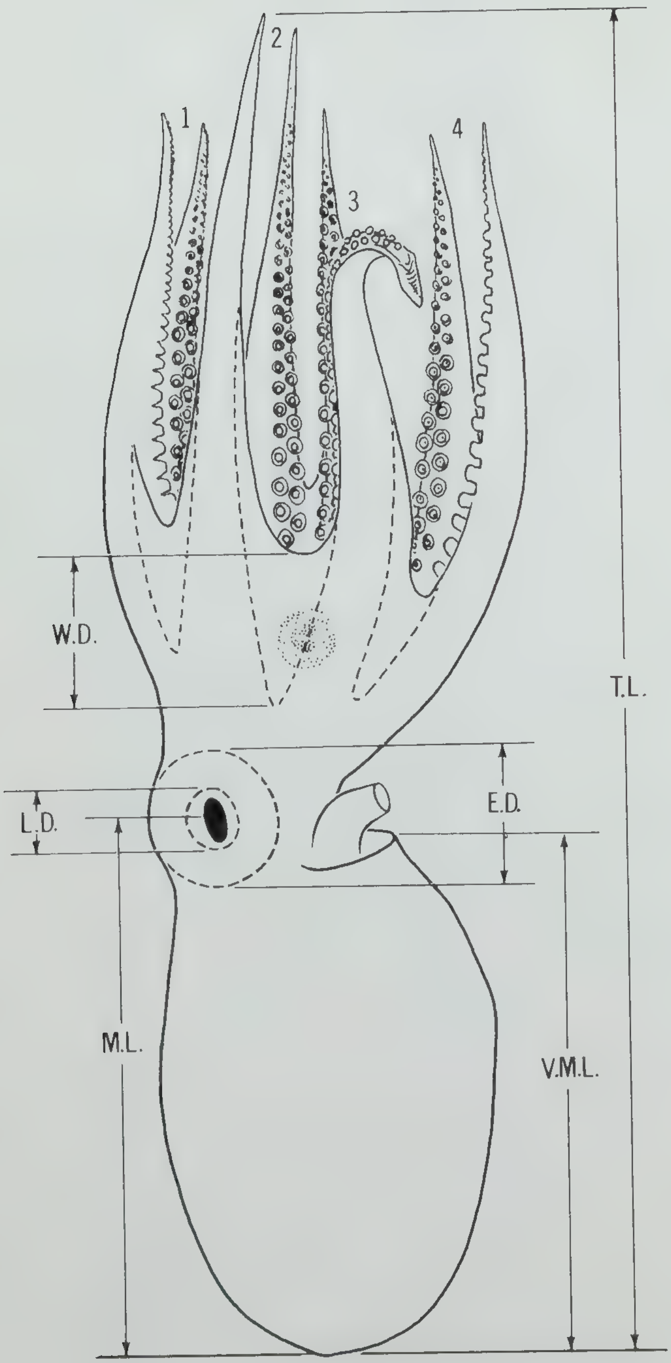
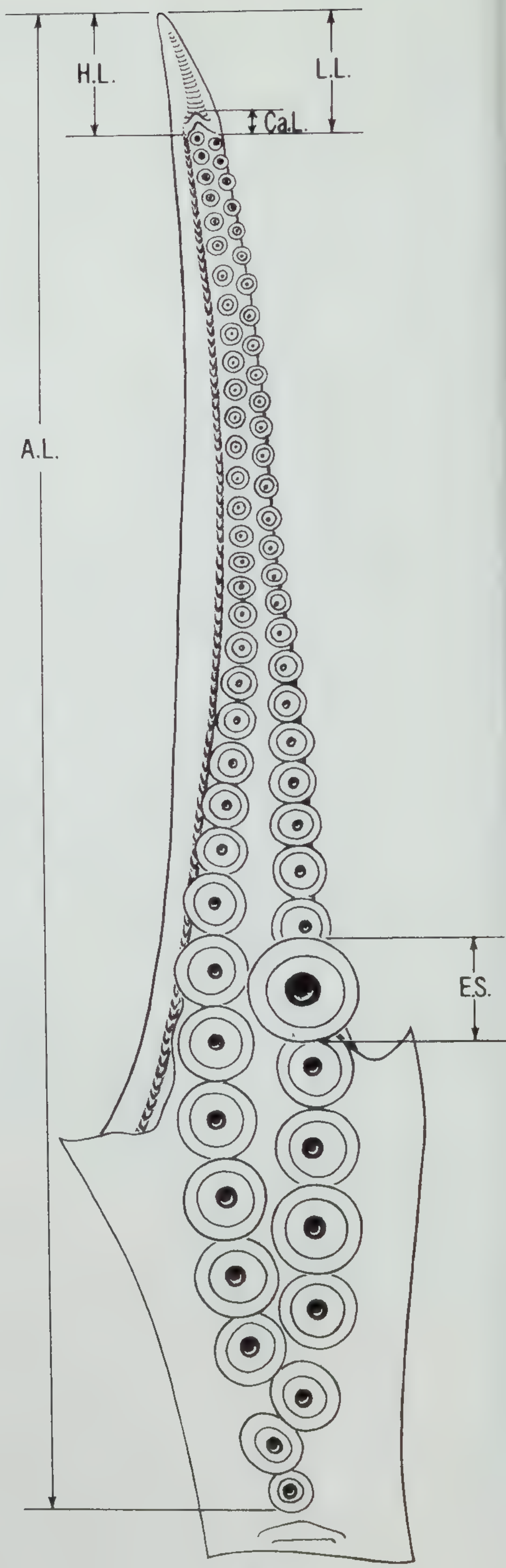

C.L.
Dactylus
Manus
C.S.
Carpus
T.L.
b

Figure 4



a



b

Appendix 3. Selected references as examples of adequate taxonomic descriptions.

SEPIOIDEA (CUTTLEFISH)

ROELEVELD, M. A., 1972. A review of the Sepiidae (Cephalopoda) of southern Africa. *Ann. South Afr. Mus.* 59(10): 193-313, 20 figures, 11 plates.

TEUTHOIDEA (SQUIDS)

BURGESS, L. A., 1967. *Loliolus rhomboidalis*, a new species of loliginid squid from the Indian Ocean. *Bull. Mar. Sci.* 17(2): 319-329, 5 figures.

COHEN, A. C., 1976. The systematics and distribution of *Loligo* (Cephalopoda, Myopsida) in the western North Atlantic, with descriptions of two new species. *Malacologia* 15(2): 299-367, 31 figures.

KRISTENSEN, T. K., 1981. The genus *Gonatus* Gray, 1849 (Mollusca: Cephalopoda) in the North Atlantic. A revision of the North Atlantic species and description of *Goantus steenstrupi* n. sp. *Steenstrupia.* 7(4): 61-99, 29 figures.

KUBODERA, T. & OKUTANI, T., 1981. *Gonatus middendorffi*, a new species of gonatid squid from the northern North Pacific, with notes on morphological changes with growth and distribution in immature stages (Cephalopoda, Oegopsida). *Bull. Nat. Sci. Mus. Ser. A* 7(1): 7-27, 4 figures, 1 plate.

ROPER, C. F. E., 1969. Systematics and zoogeography of the worldwide bathypelagic squid *Bathyteuthis* (Cephalopoda: Oegopsida). U.S. Nat. Mus. Bull. 291: 1-210, 74 figures, 12 plates.

ROPER, C. F. E. & YOUNG, R. E., 1969. A monograph of the Cephalopoda of the North Atlantic: The Family Cycloteuthidae. *Smithson. Contr. Zool.* 5: 1-24, 9 plates.

YOUNG, R. E., 1972. The systematics and areal distribution of pelagic cephalopods from the seas off southern California. *Smithson. Contr. Zool.* 97: 1-159, 38 plates.

VOSS, N. A., 1980. A generic revision of the Cranchiidae (Cephalopoda; Oegopsida). *Bull. Mar. Sci.* 30(2): 365-412, 13 figures.

OCTOPODA (OCTOPUSES)

VOSS, G. L., 1968. Octopods from the R/V PILLSBURY southwestern Caribbean cruise, 1966, with a description of a new species, *Octopus zonatus. Bull. Mar. Sci.* 18(3): 645-659, 4 figures.

VOSS, G. L., 1981. A redescription of *Octopus ornatus* Gould, 1852 (Octopoda: Cephalopoda) and the status of *Callistoctopus* Taki, 1964. *Proc. Biol. Soc. Wash.* 94(2): 525-534, 3 figures.

VOSS, G. L., 1982, *Grimpoteuthis bruuni*, a new species of finned octopod (Octopoda: Cirrata) from the southeastern Pacific. *Bull. Mar. Sci.* 32(2): 426-433, 2 figures.

Figure 4. Octopoda, Incirrata. a. Lateral View: ED = Eye Diameter, LD = Lens Diameter, ML = Mantle Length, TL = Total Length, VML = Ventral Mantle Length, WD = Web Depth. b. Hectocotylized Arm: AL = Arm Length, CaL = Calamus Length, ES = Enlarged Sucker, HL = Hectocotylus Length, LL = Ligula Length.

THE RECENT CEPHALOPODA IN THE COLLECTION OF THE NATIONAL MUSEUM OF VICTORIA

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The collection of recent cephalopods in the National Museum of Victoria dates back to its founding director, Sir Frederick McCoy. In his famous work, "Prodromus of the Zoology of Victoria" published during the period of 1878-1890, McCoy described and illustrated four species of cephalopods in detail:

Argonauta oryzata Meusch, 1787 (McCoy, 1881, p. 7-10, pl. 61-62).

Sepioteuthis australis Quoy & Gaimard, 1832 (McCoy, 1883, p. 27-28, pl. 76-77).

Ommastrephes gouldi McCoy, 1888, p. 255-257, pl. 169-170.

Sepia apama Gray, 1849 (McCoy, 1889, p. 325-327, pl. 188-190).

No serious attempt was made to acquire cephalopod specimens for the collection after McCoy, because of lack of staff interest in this group. Apart from the Port Phillip Survey conducted by the Museum in 1957-1963 when some benthic species were collected (McPherson, 1966), only occasional specimens collected by the staff or donated by the public were acquired. The recent interest in squid fisheries in Australia, the appointment of staff interested in cephalopod systematics, and the cooperation of various fisheries organizations have resulted in a significant expansion of the cephalopod collections in the Museum since 1979.

The present holdings (as of January 1983) of the cephalopod collections in the National Museum of Victoria comprises some 2,500 lots with the total number of specimens in excess of 12,000. The taxa which are well represented in the collection are Sepiidae, Sepiolidae, Loliginidae, Enoploteuthidae, Ommastrephidae, Cranchiidae and Octopodidae. The geographical coverage is Australia-wide with emphasis on south eastern Australian waters from southern Queensland to Victoria, the Southern Ocean and the Northwest Shelf of Western Australia.

At present only one cephalopod type specimen exists in the National Museum of Victoria collection:

Ommastrephes gouldi McCoy, 1888: 255-257, pl. 169, 170; F5104, HOLOTYPE

Sections of the collection has been studied and reported upon by Bell, Burn, Chapman, Gabriel, Gatliff, Macpherson, McCoy and recently by Lu, Roper and Tait.

Editor's note: The "Bibliography" section of this article is incorporated with "Bibliography of Cephalopod Biology of the Australian-New Zealand Region". See Roper (1983), pages 23-27, this volume.

THE CEPHALOPOD COLLECTIONS OF THE AUSTRALIAN MUSEUM

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The Australian Museum has large collections of cephalopods from Australian waters, some material dating back to the early part of this century. Former curators C. Hedley, T. Iredale, and J. Allan published papers on Australian cephalopods and their material including type material is available for study. S. S. Berry studied collections made in South Australia by F. I. S. *Endeavour* 1909-14 and the Mawson Australian Antarctic Expedition 1911-14, and the type material is held at The Australian Museum. Over the last decade the collections have been enlarged greatly and one major source of material has been Mr. K. Graham and his colleagues of the New South Wales State Fisheries Research Vessel *Kapala*.

Neither of the present scientists in the Department of Malacology has a research interest in cephalopods. However, it is a general policy of the department to build up our collections in all areas of molluscs and we actively encourage outside workers to use our material.

The following lists of type holdings and general holdings has been prepared as a guide to the nature of the collections.

Type Material

Cephalopod type material of species described by Allan, Berry, and Iredale and held in The Australian Museum are listed below. As only three authors are involved the holdings are listed under each author.

J. ALLAN, 1945 – TYPE MATERIAL

serventyi (Heteroteuthis); Allan, J., 1945: pp. 340-341, pl 27, figs 22, 23. C126033, HOLOTYPE.

sheardi (Eledonella); Allan, J., 1945: pp. 345-6, pl 26, figs 22-7. C126032, HOLOTYPE.

S. S. BERRY, 1917. – TYPE MATERIAL

adeliana (Moschites); Berry, 1917: pp. 17-20, pl XI, XII. C40889, HOLOTYPE.

albida (Moschites); Berry, 1917: pp. 15-16, pl X, XI. C40888, HOLOTYPE.

aurorae (Moschites); Berry, 1917: pp. 20-24, pl XII, XIII. C40891, HOLOTYPE.

harrisoni (Moschites); Berry, 1917: pp. 24-27, pl XIII, XIV. C40892, HOLOTYPE, C40893, PARATYPE.

mawsoni (Stauroteuthis); Berry, 1917: pp. 8-11, pl X. C40886, HOLOTYPE.

S. S. BERRY, 1918 – TYPE MATERIAL

australis (Rossia); Berry, 1918: pp. 253-258, pl 69, 70. E3636, HOLOTYPE.

dannevigi (Sepia); Berry, 1918: pp. 264-268, pl 73, 74. E2466, HOLOTYPE.

etheridgei (Loligo); Berry, 1918: pp. 243-249, pl 67, 69. E6068, HOLOTYPE.

galaxias (Enoploteuthis); Berry, 1918: pp. 211-221, pl 59, 60. E5723, HOLOTYPE.

hedleyi (Sepia); Berry, 1918: pp. 258-264, pl 71, 72. E2464, HOLOTYPE.

persephone (Opisthoteuthis); Berry, 1918: pp. 290-294, pl 81, 82, 85-88. E5718, HOLOTYPE.

Apparently missing

chirotrema (Sepia); Berry, 1918: pp. 268-276, pl 74, 78. E2459, HOLOTYPE. E2454, E2460, E3621, E3622, PARATYPES.

miranda (Calliteuthis); Berry, 1918: pp. 221-228, pl 61, 62. E5605, HOLOTYPE.

pluto (Opisthoteuthis); Berry, 1918: pp. 284-290, pl 81, 84. E3638, HOLOTYPE.

According to Berry the type material of the above three species should be in the museum's collections, but I am unable to find them. Apparently during World War II the wet collections were stored underground and were inaccessible for some years (W. F. Ponder – pers. comm.). During this period many specimens dried out and some were destroyed or lost. It would seem that the type material of these three species held at The Australian Museum were lost during this period.

However, as was the custom at that time Berry retained paratype material for his own collection of *Opisthoteuthis pluto* and one juvenile specimen E4375 of the material studied by Berry still survives. Unfortunately, the holotype of *Calliteuthis miranda* was a unique specimen and the material of *Sepia chirotrema*, consisting of the holotype and four other specimens cannot be found.

T. IREDALE – TYPE MATERIAL

F. Sepiidae.

bartletti (Blandosepia); Iredale, 1954: p. 67, pl 5, figs 15, 16. C133318, HOLOTYPE.
baxteri (Blandosepia); Iredale, 1940: p. 442. C133317, HOLOTYPE.
braggi xera (Arctosepia); Iredale, 1954: p. 74, pl 5, figs 19-21. C133310, HOLOTYPE; C102192, PARATYPES (5).
eclogaria (Ponderosepia); Iredale, 1926: p. 239, pl 35, figs 7-8. C19085, HOLOTYPE.
ellipticum adjacens (Acanthosepion (Fiscisepia)); Iredale, 1926: p. 239, pl 35, figs 5, 6. C133302, HOLOTYPE; C133303, PARATYPES (4).
gemellus (Glyptosepia); Iredale, 1926: p. 192, pl 22, figs 1, 2. C133306, HOLOTYPE.
genista (Solitosepia); Iredale, 1954: p. 66, pl 5, figs 17, 18. C133309, HOLOTYPE.
hulliana (Crumenasepia); Iredale, 1926: p. 239, pl 35, figs 1, 2. C133333, HOLOTYPE.
lana (Solitosepia); Iredale, 1954: p. 66. C133301, HOLOTYPE.
liliana (Solitosepia); Iredale, 1926: p. 188, pl 21, figs 1-3. C133300, HOLOTYPE. C133327, PARATYPE?
limata (Arctosepia); Iredale, 1926: p. 193, pl 23, figs 7, 8. C133316, HOLOTYPE.
macandrewi (Mesembrisepia); Iredale, 1926: pp. 190-1, pl 21, figs 8, 9. C133328, HOLOTYPE.
macilenta (Glyptosepia); Iredale, 1926: p. 192, pl 22, figs 3, 4. C133305, HOLOTYPE.
melwardi (Sepiella); Iredale, 1954: p. 78, pl 5, figs 1-6. C133320, HOLOTYPE; C133321, PARATYPE.
opipara (Glyptosepia); Iredale, 1926: p. 191, pl 22, figs 7, 8. C133330, HOLOTYPE.
ostanes (Mesembrisepia); Iredale, 1954: p. 69, pl 4, figs 5, 6. C133311, HOLOTYPE.
pageorum (Acanthosepion); Iredale, 1954: p. 76, pl 4, figs 7-9. C133315, HOLOTYPE.
parysatis (Amplisepia); Iredale, 1954: p. 71, pl 4, figs 1-2. C133307, HOLOTYPE.
plangon adhaesa (Solitosepia); Iredale, 1926: p. 238. C133304, HOLOTYPE.
rozella peregrina (Solitosepia); Iredale, 1926: p. 238. C133322, HOLOTYPE; C133323, PARATYPE.
pfefferi laxior (Metasepia); Iredale, 1926: p. 240, pl 35, figs 9, 10. C133326, HOLOTYPE; C19084, PARATYPES (2).
pfefferi wanda (Metasepia); Iredale, 1954: p. 78, pl 5, figs 9-11. C133314, HOLOTYPE.
rhoda (Arctosepia); Iredale, 1954: p. 75, pl 4, figs 10-12. C133319, HOLOTYPE.
rex (Decorisepia); Iredale, 1926: p. 193, pl 22, figs 9, 10. C127593, HOLOTYPE.
rozella (Solitosepia); Iredale, 1926: p. 190, pl 21, figs 6, 7. C133336, HOLOTYPE.
submestus (Solitosepia); Iredale, 1926: p. 238, pl 35, figs 3, 4. C133325, HOLOTYPE.
treba (Arctosepia); Iredale, 1954: p. 75. C133324, SYNTYPES.
versuta (Arctosepia); Iredale, 1926: p. 194, pl 23, figs 5, 6. C133313, HOLOTYPE.
whitleyanum (Acanthosepion); Iredale, 1926: p. 195, pl 23, figs 9, 10. C133331, HOLOTYPE.

F. Nautilidae

repertus (Nautilus); Iredale, 1944: pp. 295-6. C63202, HOLOTYPE.

Non-Type Material

In addition to the type material the Australian Museum holds a large collection of non-type cephalopod material. Apart from the sepiid collection which, due to its large number and importance, will be listed separately, the general collection consists of over 1000 lots of specimens. Sepiolidae, Loliginidae, Enoploteuthidae, Ommastrephidae, Cranchiidae and Octopodidae are well represented in the collection. The collection is Australia-wide in coverage with emphasis on the material from the east coast particularly the waters off New South Wales.

F. Sepiidae Keferstein, 1866.

The sepiid collections are large and impor-

tant, with 28 Iredale holotypes and 2 Berry holotypes, which are listed separately. The general collection contains in excess of 250 lots of preserved animals, usually each lot containing multiple specimens, and extensive holdings of cuttlebones, mainly from Australian waters. Most of the preserved material is unidentified but it is probably that specimens of most of Iredale's proposed species are present. The cuttlebone collection is of historical importance, containing all the comparative material Iredale worked with, and large ranges of specimens collected since Iredale's time. Even with Iredale's type material it is impossible to distinguish some of his species from each other, and it is obvious in other cases that older names have precedence. Unfortunately, Dr W. Adams, the most productive worker in recent years on the Indo-West Pacific Sepiidae, has been unable to study the large sepiid collections available at The Australian Museum. Until this is done, many problems will remain in the taxonomy of this group in the Indo-West Pacific. The cuttlebones in the collection have been identified by reference to Iredale's types, and the works of Adam and other authors. Possible synonyms are listed where it is impossible to sustain Iredale's species differences on examination of large series of cuttlebones. These suggested synonymies will only be verified when anatomical studies are undertaken and are only included to indicate the extent of the taxonomic confusion prevailing.

Following Adam & Rees (1966), Iredale's many generic and subgeneric names are considered superfluous.

Sepia apama Gray, 1849 = *Amplisepia verreauxi* Iredale, 1926 (non Rochebrune).
= *Amplisepia parysatis* Iredale, 1954: Many lots.

Sepia bartletti Iredale, 1954: One lot possibly PARATYPE material.

Sepia baxteri Iredale, 1940: 2 lots including large PARATYPE series.

Sepia braggi Verco, 1901: Iredale's *Arctosepia* group are difficult to distinguish externally. Lots belonging to this group include specimens identified in the past under the following names which may prove synonymous:

S. braggi Verco, 1901. PARATYPE.
S. braggi xera (Iredale, 1954). PARATYPE.
S. limata (Iredale, 1926).
S. mira Cotton, 1932.
S. rhoda (Iredale, 1954).
S. treba (Iredale, 1954).
S. versuta (Iredale, 1926).

Sepia chirotrema Berry, 1918: 7 lots.

Sepia cultrata Hoyle, 1885
= *Glyptosepia gemellus* Iredale, 1926.
= *Glyptosepia hedleyi* (Berry, 1918).
= *Glyptosepia hendryae* (Cotton, 1929). Many lots.
= *Glyptosepia macilenta* Iredale, 1926.

Sepia elliptica Hoyle, 1885 = *Acanthosepion ellipticum adjacens* Iredale, 1926. Many lots.

Sepia latimanus Quoy & Gaimard, 1832 = *Ponderosepia eclogaria* Iredale, 1926. Many lots.

Sepia mestus Gray, 1849 = *Solitosepia liliana* (Iredale, 1926). Not *S. mestus* Iredale, 1926. Many lots.

Sepia mestus Iredale, 1926: Many lots (not *S. mestus* Gray, 1849).

Sepia novaehollandiae Hoyle, 1909 = *Mesembrisepia irvingi* Meyer, 1909. Many lots.

Mesembrisepia macandrewi Iredale, 1926.
= *Mesembrisepia ostanes* Iredale, 1954.

Sepia opipara Iredale, 1926: Many lots.

Sepia papuensis Hoyle, 1885
= *Solitosepia galei* Meyer, 1909.
= *Solitosepia genista* Iredale, 1954.
= *Solitosepia glauerti* Cotton, 1929.
= *Solitosepia occidua* Cotton, 1929.
= *Solitosepia submestus* Iredale, 1926. Many lots.

Sepia pharaonis Ehrenberg, 1831
= *Crumenosepia hulliana* Iredale, 1926.
= *Crumenosepia ursulae* Cotton, 1929. Many lots.

Sepia plangon Gray, 1849: Many lots.

Sepia rex (Iredale, 1926): Many lots.

Sepia rozella (Iredale, 1926): Many lots.

Sepia smithi Hoyle, 1885 = *Acanthosepion pageorum* Iredale, 1954. Many lots.

Sepia whitleyana (Iredale, 1926): Many lots. (Adam & Rees, 1966, consider this close to *S. elliptica*, and the specimen they figure is *S. elliptica* not *S. whitleyana*).

Sepia (Metasepia) pfefferi Hoyle, 1855: 15 lots.

Sepiella melwardi Iredale, 1954: 3 large lots including possible PARATYPE series.

Editor's note: The "Bibliography" section of this article is incorporated with "Bibliography of Cephalopod Biology of the Australian-New Zealand Region". See Roper (1983), pages 23-27, this volume.

THE CEPHALOPOD COLLECTION OF THE WESTERN AUSTRALIAN MUSEUM

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1. History of the Collection

The cephalopod collection of the Western Australian Museum had its origin in a few dry specimens which had been in the collection of the Perth Museum when, in 1897, its name was changed to the Western Australian Museum and Art Gallery and the cataloguing of its collections commenced.

Additions to this section of the collections was slow at first, but the nucleus of the wet cephalopod collection was apparently formed by some octopus from the Swan River and from Fremantle which were donated by an interested amateur in 1899. The interest of, and the support by the public has been a significant factor in the growth of this collection since that time.

In 1910 and again in 1912 the size of the Museum staff was increased and active collecting began. W. B. Alexander in his position as Assistant in Natural History and later as Keeper of the Department of Biology collected in local waters, and took part in collecting activities aboard F.I.S. *Endeavour* when she visited Western Australian waters in 1912. After Alexander's resignation in 1920 L. Glauert, who had been initially appointed as Assistant in Natural History and Ethnology, and was later promoted to the position of Keeper of Geology and Ethnology, became more involved with marine groups. After being promoted, in 1928, to the position of Curator of the Museum and later to the position of its Director, Mr Glauert assiduously collected on local beaches and encouraged the enthusiasm of local collectors. Active interaction with the public and with Government departments and instrumentalities was further stressed by Glauert's successor Dr W. D. L. Ride. As the Museum entered into a phase of rapid growth, marine collecting programs were carried out in the early 1960's by the Museum's first Curator of Invertebrates, and from the mid-1960's onwards by the staff of the department of Molluscs (later Malacology). Field work within Western Australia, along the coasts of other Australian states and in countries within the central Indo-West Pacific Region (such as Indonesia, Malaysia and the Philippines) has brought about a rapid increase in the size and coverage of the cephalopod collection. Staff members of other marine departments within the Museum have also contributed significantly to these collections both during interdisciplinary surveys and during their own field programs.

Since the Hamburg Expedition to south-western Australia in 1905, foreign workers collecting in our waters have responded to the State's need for reference material. In 1911 Drs Michaelson and Hartmeyer, who had lead the Hamburg Expedition, donated some of their specimens to this Museum. One of these is a paratype of the cuttlefish *Sapia irvingi* described by Meyer in 1909 in the expedition report, *Fauna Südwest-Australiens.* Since that time Hawaiian collectors on board the chartered fishing vessel *Davena*, Japanese scientists with the fisheries research and training ship *Umitaki Maru* and those engaged in fisheries surveys aboard various commercial Taiwanese vessels have donated material, particularly from waters off the northern coasts of Western Australia. Specimens have also been donated by collectors and researchers working in other Australian states, the Philippines, and in Singapore.

Since early 1903 many specimens have been added to the collections because of the interests and enthusiasm of the directors and officers of the WA Dept of Fisheries and Fauna (later Fisheries and Wildlife). The support of this department and the fishing companies with which it collaborates, has provided specimens from the waters off the Recherche Archipelago to those off the eastern Kimberley region during

surveys connected with rock lobster, prawn and scale fisheries and with the policing of foreign vessels inside territorial waters since the early 1960's. More recently, exploratory fishing on cephalopod stocks has provided many specimens and much valuable data from many areas along the long Western Australian coastline. In addition, that Department's provision of ship time for Museum activities has enabled Museum staff to collect in areas from Cockburn Sound to Shark Bay more intensively and with greater attention to detail than would be otherwise have been possible.

Federal departments and instrumentalities have been similarly helpful. Research on the whale stocks which were fished off the southern coast of Western Australia, on the interaction of rock lobsters and octopus at the Houtman Abrolhos and adjacent mainland coast and on the potential scale fisheries in the Great Australian Bight provided a large number of Specimens. Museum staff were able to join the frigate HMAS *Diamantina* on a number of training voyages between 1963 and 1976 and to carry out dredging programs on the continental shelf and slope of the western coast.

In 1976 Museum staff were given time on the CSIRO chartered vessel *Sprightly* to dredge across the shelf, south of the Houtman Abrolhos, resulting in the collection of a number of benthic cephalopod specimens. In 1978-82 Museum staff were given places aboard the CSIRO chartered vessels *Courageous* and *Soela* during voyages to survey the fauna of the North West Shelf. These activities provided specimens from the more shallow waters of the shelf and also specimens of taxa previously uncollected from the deeper waters of the slope.

2. Research work on the cephalopods of Western Australian waters

Records of cephalopods in Western Australian waters date from the 17th century, when descriptions of floating cuttlebones, taking to denote the proximity of land, were made in the area off Shark Bay by an employee of the Dutch East Indies Company and later by Dampier in his second voyage to Australia (*fide* Alexander, 1914). Octopus at Bernier Island, Shark Bay were noted by Péron (1807) during the voyage of the *Geographe* and *Naturaliste* and from Péron's notes, an octopus from nearby Dorre Island was later described by Lesueur (1821) under the name *Sepia boscii*, and later still by de Blainville (1826) under the name of *Polypus variolatus.*

Cephalopods and other molluscs were collected from the western coasts of the continent by P. P. King during his surveys aboard the *Mermaid* and later the *Bathurst* between 1817 and 1822 (King, 1826). His specimens were sent back to Gray in the British Museum who apparently later (Gray, 1849) localised them only as having been taken in New Holland, which was the term commonly applied to that part of the continent west of latitude 135°E.

During the voyage of the French ships *Uranie* and *Physicienne*, a squid was collected in September, 1818 off the coast near Shark Bay (then known as Endracht's or Eendracht's Land) and was later described as *Loligo uncinata* by Quoy and Gaimard (1825), two medical officers who also acted as naturalists.

Following the settlement of the Swan River Colony a German naturalist and collector Dr J. A. L. Preiss travelled during 1839-40 throughout the south western corner of the country collecting specimens. He sent the molluscs home to Menke, who in 1843 published an account of the 263 species he had received, one of which was a specimen of *Nautilus pompilius*, from Port Leschenault (Bunbury) — a locality apparently well south of the distributional range of the species but within the area over which drift shells have subsequently been found.

Germans again visited Western Australia to collect marine specimens in 1875. The *Gazelle* travelled along the north west coast, and dredging operations in Mermaid Strait yielded a myopsid squid later identified by von Martens (1889) as *Sepioteuthis australis* (Quoy and Gaimard).

When Brazier in 1892 published his *Catalogue of Australian Cephalopods* he listed two species of cuttlefish, *Sepia rostrata* and *S. indica* and one species of octopus, *Polypus boscii*, from Western Australian waters. He also recorded the oegopsid squid *Symplectoteuthis oualaniensis* from the pearling grounds of Nicol Bay.

As mentioned above, the report on the cephalopod molluscs collected by the Hamburg Expedition were published by Meyer in 1909. Along with the cuttlefish *Sepia latimanus* Quoy and Gaimard and one tentatively identified as *S. braggi* Verco Meyer described two new cuttlefish, *S. irvingi* from Cockburn Sound and *S. galei* from Shark Bay. In addition he recorded the Western Australian occurrence of the sepiolid *Sepioloidea lineolata* Quoy and Gaimard.

A Swedish expedition lead by Dr E. Mjöberg visited the pearling grounds near Broome and off Cape Jaubert between 1910 and 1913 and the molluscs collected there were reported upon by Odhner (1917). The only cephalopods collected there were four specimens of octopus which Odhner identified as *Octopus membranaceus* Quoy & Gaimard and *O. cuvieri* d'Orbigny.

In 1910-1911 Dr J. C. Verco of South Australia and his friend Dr Torr travelled through the south and southwest of the state. Then in 1912 Verco joined the *Endeavour* under the fisheries biologist Dannevig and travelled to the western part of the Bight. The results of the trawling and dredging operations carried out by this vessel were later published, the cephalopod collections being described by Berry (1918). Verco (1912) recorded *Spirula* from Geraldton, while Berry recorded the cuttlefish *Sepia hedleyi* n. sp. the oegopsid *Nototodarus gouldi* McCoy, the sepiolid *Rossia* (*Austrorossia*) *australis* n. sp., the octopus *Polypus variolatus* and the cirrate octopod *Opisthoteuthis pluto* n. sp. from W.A. waters off Eucla and the cuttlefish *S. dannevigi* from Cape Naturaliste to Geraldton.

In 1914 Robson had published a short paper on two species of cephalopod which had been taken in the Monte Bello Islands and forwarded to him by collectors interested in that area. One was a new species of dumpling squid *Sepiadarium auritum* and the other an unidentified species of *Octopus*.

Just a year later a checklist of the molluscs of Western Australia compiled by Hedley was read to the Royal Society of Western Australia and was published in the following year (Hedley, 1916). This summarised all Western Australian molluscs recorded in the literature as well as those present in the collections of the Australian Museum and the British Museum (Natural History) to that time.

The next contribution to knowledge of this fauna was a paper by Cotton (1929) in which he reported on a collection of cuttlebones forwarded to him by the then Curator of the Museum, L. Glauert. Collected mainly on beaches around Perth and Fremantle, the cuttlebone collection contained ten species. *Solitosepia glauerti*, *S. hendryae*, *S. occidua*, *Decorisepia cottesloensis*, and *Crumenasepia ursulae* were described as new species from this collection, while *Mesembrysepia novaehollandiae* (Hoyle), *M. chirotrema* (Berry), *Glyptosepia hedleyi*, *Arctosepia braggi* (Verco) and *Amplisepia apama* (Gray) were also recorded. Cotton and Godfrey (1940) repeated most of these records.

Robson in 1929 published his massive monograph on the octopods in which he records British Museum specimens of the blue-ringed octopus *Hapalochlaena lunulata* (Quoy and Gaimard) from the Swan River [Colony]. In this publication he also discusses the validity of the octopus species *O. boscii* and *O. variolatus*.

Cuttlebones were again the subject of a paper by Iredale (1954), in which he described the new species *Solitosepia genista* from Broome and *Amplisepia parysatis* from Shark Bay as well as giving new information on distributional range and relationships of other species. Some of this data was obtained from specimens in the collection of the W.A. Museum.

In discussing the fatal bite of an octopus in Darwin, Flecker and Cotton (1955) record the occurrence of *Octopus pallidus* Hoyle, *O. australis* Hoyle, *O. lunulata*, *O. maculosa* Hoyle and *Bentheledone rotunda* (Hoyle) in Western Australia. Their identification of the venomous octopus as *O. rugosus* Bosc was disputed later by McMichael (1964) who identified it as *Hapalochlaena lunulata* and for this species he gave a distribution from the northwest coast of Australia to the islands to the north.

It was at about this time that cuttlebones and some wet specimens of cuttlefish were first sent to Professor Adam in Belgium for assistance

with identification. As more material became available this was forwarded and in 1979 Adam published a paper on the sepiid collection of the W.A. Museum.

In 1966 Clarke's work on oceanic squid was published. Although he did not give details of records (other than literature records) on which he based his distributional data, he did indicate a possible or definite presence of a number of diverse oegopsid squid species off the south of Western Australia. Filippova (1971) again did not give details of locality records though collecting stations of USSR research vessels were indicated off the southwest coast of W.A.

During the latter part of the 1970's L. Joll was publishing the results of his work on the biology of *Octopus tetricus* Gould which had been considered an important predator on the commercial rock-lobster in the south-west of W.A. (Joll 1976, 1977, 1978).

The most recent work on cephalopods of W.A. waters is included in the identification guide to Austraian ommastrephids by Lu and Dunning (1982). Records from the collections of the W.A. Museum have been used in the composition of distributional maps of a number of species which are recorded from the south east Indian Ocean for the first time.

3. Present Composition of the Collection

As of March, 1983 the cephalopod collection of the Western Australian Museum consists of approximately 1100 lots of preserved animals, 400 lots of dry specimens (cuttlebones, *Nautilus* and *Spirula* shells, and egg cases of argonauts) and 800 lots of squid beaks, the latter having been collected from the stomach contents of whales.

The cuttlefish collection is almost completely identified, those specimens which have been added since Adam's work was completed have, in general, only added more detail to the known geographic ranges of recorded species. A few species have had their known geographic range considerably extended.

Some of the sepiolids and sepiadariids are currently being examined by C. C. Lu. Among these are the only known specimens of *Sepiadarium auritum* other than the type specimen.

The octopod collection is largely unidentified. Some of the *Hapalochlaena* collection is being worked upon by G. Voss, and the small collection of *Argonauta* species is identified. The remainder awaits the attention of workers willing to tackle the systematics of this difficult group. This is possibly one of the most neglected areas in molluscan systematics.

The squid collection is considerable and is, in general, fairly well identified. Specimens in the collection in 1975 were identified by C. Roper, and C. C. Lu identified many of the more recently collected specimens in 1981.

Specimens collected between 1979 and 1982 on the north west shelf are of particular interest, particularly those collected from the area of the slope to about 700 metres. Many of these are quite new to the collection and most of those identified indicate considerable extensions in known geographic ranges. It is obvious that a considerable effort needs to be made in sampling this fauna.

Some advance has been made in the state of knowledge about the pelagic species of squid on the continental shelf which have been surveyed for their fisheries potential. However, the benthic fauna of most of the State's continental shelf outside sheltered embayments is virtually unknown, particularly on the western and northern coasts.

The large collection of squid beaks has been and is being worked upon to determine species composition, and to extract other data appropriate to the needs of the International Whaling Commission. This collection of squid beaks has not been accessed into the general collection.

With all groups attention is being given to building up a record of colour notes and particularly of colour slides cross-catalogued to particular specimens.

Type Specimens

Sepia cottoni Adam, 1979: 193-200, pl. 11, figs. 1-6.

Holotype: CSIRO Stn. 46, W of Lancelin, WA (31°54′S, 114°55′E), 114-122 m; leg. HMAS *Diamantina*; 1755 hrs, 5 February, 1964; WAM 435.65: 1♂ in spirit.

+ *Paratypes*

Sepia reesi Adam, 1979: 200-201, pl. 4, fig. 3.
Holotype: Salmon Bay, Rottnest I., WA; leg. L. Glauert; September 1931; WAM 497-76: 1 dry shell.
+ *Paratypes*

Sepia vercoi Adam, 1979: 190-193, pl. 10, figs. 5, 6.
Holotype: CSIRO Stn. 200, W of Shark Bay, WA (25°31′S, 112°29′E), 130 m; leg. HMAS *Diamantina*; 0220 hrs, 9 October, 1963; WAM 441.65: 1 ♂ in spirit.
+ *Paratypes*

Sepia irvingi Meyer, 1909: 333, figs. 7-10.
Paratype: Warnbro Sound, W.A. leg. Hamburg Expedition; (labelled Dec. 1910, presumably collected in 1905); WAM 4203: 1 in spirit.

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* Much of this section is incorporated with "Bibliography of Cephalopod Biology of the Australian-New Zealand Region". See Roper (1983), pages 23-27, this volume. — Editor's note.

THE CEPHALOPOD COLLECTION IN THE SOUTH AUSTRALIAN MUSEUM

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Introduction

The aim of this paper is to provide a general account of the South Australian Museum cephalopod collection and to indicate the current range of the South Australian fauna.

The bulk of the South Australian Museum (SAM) mollusc collection was collected by Sir Joseph Verco during the years 1890-1912, most of it was dredged or beach collected. Verco was a dedicated conchologist who took little interest in the animals of the shells he studied; therefore it is not surprising that he described only one new cephalopod—*Sepia braggi* (Verco, 1907) from a cuttlebone washed up on a metropolitan beach. Because both Verco and his successor, B. C. Cotton, were conchologists the collection of cephalopods in SAM is unrepresentative of the State's fauna. The collection consists of about 300 lots of spirit specimens and 22 drawers of dry cuttlebones, mainly representing a few common species. Recent additions have improved the collection, but these have been limited as there have never been any experimental trawling operations in S.A. like those of C.S.I.R.O., Fisheries Departments and others which have occurred in Western Australia and the eastern States. However, there is currently an intensive effort by the author, with the help of the S.A. Fisheries Department and others, to add to the collection and make it available to interested specialists.

RESUME OF SAM COLLECTION

There are currently 28 species of cephalopods known to occur in South Australian waters, a small number that reflects limited collecting efforts. Most are inadequately known because of the lack of specimens and the lack of taxonomic background in cephalopods by earlier researchers. These workers seemed to copy each other, often without checking the literature or comparing specimens. For example much of Cotton and Godfrey (1940) is taken directly from Berry (1918; 1921) and others.

Many of the sepioidea are known only from a few specimens and in the Sepiidae the animal often is unknown. Frequently descriptions and illustrations are inadequate or inaccurate and the range of specific variation rarely was discussed. Iredale's (1920) new genera based only on cuttlebones and subsequent authors only added to the confusion. A revision of Australian Sepioidea therefore is urgently needed. The SAM collection of Sepioidea is not very large and consists of 22 drawers of dry cuttlebones and about 150 lots of spirit specimens. The cuttlebones are generally in poor condition and represent mainly *Sepia apama*, *S. novaehollandiae* and some *S. braggi* with a selection of eastern and northern Australian species. The spirit specimens consist mainly of *S. apama*, *Sepioloidea lineolata* and *Euprymna tasmanica* but there are also a few lots of *S. braggi*, *S. novaehollandiae* and *Idiosepius notoides*. Other southern Australian species such as *Sepia chirotrema*, *S. jaenschi* and *Rossia australis* are represented by only one or two lots. There are no spirit specimens of *Spirula*; only a few shells found washed up on metropolitan and South-East beaches. *Sepia dannevigi* Berry 1918, *S. hedleyi* Berry 1918 and *Sepiadarium austrinum* Berry 1921, originally described from S.A. are not represented in the SAM collection.

In southern Australia the Teuthoidea are well represented by *Sepioteuthis australis* although SAM has few well preserved specimens but the oceanic squid (Oegopsida) are not well known because little sampling has been done. Clarke (1966) reviewed the group and indicated the lack of knowledge of Australian species by the many blank spaces on his distribution maps. Most Australian records are by Berry (1918) and Allan (1945). Only three species,

Nototodarus gouldi, *Ommastrephes bartrami* and *Taningia danae* are known from S.A. and these are known only from recent collections. Adequate collecting will surely reveal the presence of many more species, as they occur in Australian waters in general. The SAM collections of Teuthoidea, some 50 lots, consist mainly of *S. australis* and *N. gouldi* with a few *O. bartrami* and two specimens of *T. danae* (Zeidler, 1981).

The octopods also have been a neglected group in Australia. Robson (1929; 1931) reviewed the Australian octopods, but no thorough study has been made since. Most of the known species need verification and many new species await description. The SAM collection of octopods, about 100 lots, consists of mainly unidentified specimens although *Hepalochlaena maculosa*, *Octopus pallida* and *O. flindersi* are well represented. There are also a few interesting specimens such as *Ocythoe tuberculata* (1 ♀ and 1 ♂), *Grimpella thaumastocheir* (♂) and *Opisthoteuthis* sp. (two specimens).

The majority of the small collection of cephalopods collected by the BANZ Antarctic Research Expedition, 1929-1931 (Dell, 1959) is also housed in SAM.

HISTORICAL BACKGROUND TO SPECIES RECORDED FROM S.A.

The first records of cephalopods from S.A. are by Angas (1865) who noted two species, *Argonauta nodosa* (listed as *A. oryzata*) and *Spirula spirula* (listed as *Ammonia laevis*). These two species are rarely found on South Australian beaches. Angas made no mention of cuttlebones, even though numerous specimens occur on the beaches. Brazier (1892) added four more species to the South Australian fauna; one octopus, *Hapalochlaena maculosa* (listed as *Octopus pictus*), and three sepiids, *Sepioloidea lineolata*, *Sepia apama* and *S. novaehollandiae* (listed as *S. australis*). Verco (1907) described only one new cephalopod, *Sepia braggi*. Riddle (1920) recorded the first *Nautilus* from South Australia, *N. repertus* (as *N. pompilius*); this remains the only record. However, Berry (1918; 1921) made the most notable additions to the cephalopod fauna of Australia adding seven new species to the South Australian fauna—*Sepia hedleyi*, *S. dannevigi*, *S. chirotrema*, *Opisthoteuthis pluto*, *O. persephone*, *Sepiadarium austrinum* and *Idiosepius notoides*.

Verco and Cotton (1928) produced the first comprehensive list of South Australian cephalopods, a total of 20 species, three of which were included because they were found in adjacent waters and probably occurred in South Australia: *Rossia australis* verified by Cotton (1938), *Octopus pallidus* (listed as *Polypus variolatus*) verified by Cotton (1932), and *Nototodarus gouldi* verified only recently by a specimen caught 0.5 km off Hallet Cove, St Vincent Gulf in 1964 (unpublished record). Another two, *Sepioteuthis australis* and *Euprymna tasmanica*, were new records. Surprisingly *S. australis*, probably the most common cephalopod in South Australian inshore waters, was not recorded earlier. Cotton described two more new species; *Sepia jaenschi* (1931) and *Octopus flindersi* (1932) before combining with Godfrey to produce their 1940 monograph of South Australian molluscs in which they erroneously include 13 species, some of which do not even belong to the Australian fauna. Their publication should be used therefore with extreme caution. Only one cephalopod, *Octopus australis*, was a new record for the State. Since 1940 no one has worked on South Australian cephalopods and only three species of note have been added to the collections: *Ocythoe tuberculata* washed up at Port MacDonnell, the first record of this species in Australia (Roper & Sweeney, 1975), *Taningia ?danae* found floating offshore near Port Lincoln in 1980, the first record of a complete specimen from Australia (Zeidler, 1981) and *Ommastrephes bartrami* a photo of which Cotton (1960) mistook for a large specimen of *Nototodarus gouldi*.

LIST OF CEPHALOPOD TYPES IN SAM

A more detailed list is given by Zeidler and Macphail (1978). The Sepiidae are represented only by cuttlebones.

Crumenasepia ursulae Cotton, 1929. *J. Proc. R. Soc. W. Aust.*, **15**: 90-91, pl. 15, figs. 3, 4. HOLOTYPE and three PARATYPES.

=*Sepia pharaonis* according to Adam & Rees (1966).

Decorisepia cottesloensis Cotton, 1929. *J. Proc. R. Soc. W. Aust.*, **15**: 90, pl. 16, figs. 1, 2.
HOLOTYPE only.
=?*Sepia rex* according to Adam (1979).

Decorisepia jaenschi Cotton, 1931. *S. Aust. Nat.*, **12**(3): 41, figs. 5, 6.
HOLOTYPE only.
=*Sepia jaenschi* according to Adam & Rees (1966).

Sepia braggi Verco, 1907. *Trans. Roy. Soc. S. Aust.*, **31**: 213, pl. 27, figs. 6a-d.
HOLOTYPE and four PARATYPES.

Solitosepia glauerti Cotton, 1929. *J. Proc. R. Soc. W. Aust.*, **15**: 87, pl. 14, figs. 3, 4.
HOLOTYPE only.

Solitosepia hendryae Cotton, 1929. *J. Proc. R. Soc. W. Aust.*, **15**: 87-88, pl. 15, figs. 1, 2.
HOLOTYPE only.

Solitosepia occidua Cotton, 1929. *J. Proc. R. Soc. W. Aust.*, **15**: 88, pl. 14, figs. 1, 2.
HOLOTYPE only.

Tenuisepia mira Cotton, 1932. *Rec. S. Aust. Mus.*, **4**(4): 546-547, figs. 7-9.
HOLOTYPE only.
=*Sepia mira* according to Adam & Rees (1966).

Octopus flindersi Cotton, 1932. *Rec. S. Aust. Mus.*, **4**(4): 543-544, fig. 6.
HOLOTYPE only—Cotton believed this to be a female as the hectocotylus is not evident but upon dissection the type proved to be a male (Boletzky, pers. comm.).

Editor's note: The "Bibliography" section of this article is incorporated with "Bibliography of Cephalopod Biology of the Australian-New Zealand Region". See Roper (1983), pages 23-27, this volume.

FOOD, FEEDING AND GROWTH IN CEPHALOPODS

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Abstract

Cephalopods play an important role in the food web of the oceans. While their predators are fairly well known, little is known about their prey and almost nothing about these caloric values. Stomach contents analysis and rearing experiments provide information of about 50 species out of the 700 known to exist. Crustaceans are the main food item, followed by fish and molluscs, including cephalopods. In many species, prey change with increasing size of the predator while others prefer the same food, e.g. crustaceans, during their whole life cycle.

Young benthic octopuses eat 10 to 20% of their own body weight per day. In later stages the food intake decreases to 5-2%. In young pelagic squids, the food intake is about 50% and 10-20% in subadult and adult animals. Their higher food intake can be related to the higher metabolic costs.

The conversion rate is very high: on a wet weight basis, 20-60% of the ingested food is used for growth. Food intake depends on temperature while conversion rate does not, but both seem to be dependent upon food quality, at least in some species.

Growth is very fast in young animals, slows down in subadults and adults and stops altogether or even declines in mature animals, especially in octopodid females.

The question of whether growth models obtained from laboratory data can be applied to growth in field populations is discussed.

Introduction

Elucidating the role of high-level predators in marine ecosystems is one of the urgent problems in fisheries biology, as has been clearly shown during the discussions of the workshop on 'The Biology and Resource Potential of Cephalopods' held in Melbourne in March 1981. There is no doubt that cephalopods are high-level predators, and the vital role that they play in the food web of the oceans, in pelagic as well as in benthic communities, has become increasingly evident during the last two decades. Cephalopods are heavily preyed upon by fish, birds and marine mammals, especially by whales, some of which depend almost exclusively upon squids as food (Clarke, 1977, 1980). A good deal is known about cephalopod predators, and analysis of their stomach contents allow us to make fairly realistic estimations of the stock size of some cephalopods. But our knowledge of the prey of cephalopods in the field is still poor. The range of prey organisms is wide, as representatives of nearly all marine phyla figure among them. The most important appear to be crustaceans, fish and molluscs, including cephalopods. A wealth of information exists on the food of maintained and reared cephalopod species (Boletzky, 1974a; Yang *et al.* 1980; Boletzky & Hanlon, this volume). However, even for these species, verifications from field observations are scarce. Under laboratory conditions, cephalopods may accept food that they never encounter in their habitat.

As recent work shows (for a review, see Mangold, *et al.*, in press) the growth of cephalopods is fast. The life cycles are short, varying from about 6 months in small species to one, two or three years in larger ones. A few species of very large adult size may live for five or six years. Cephalopods are semelparous animals, reproducing once in their life time, although this 'once' may span quite a long period in some species. Indeed, spawning may be interrupted for several weeks (Mangold-Wirz, 1963; Boletzky, 1974a; Hixon, 1980).

If we ever hope to establish an 'energy balance sheet' between the predators and the prey of cephalopods, we have to determine specific energy budgets for growing cephalopods to adult size. This certainly will vary among different species and may depend, among other factors, on the kind of prey that each species eats. I do not intend to cover the whole topic here—it would indeed be a gigantic task. This paper constitutes a mini-review treating only certain aspects of food, feeding behaviour and feeding rate, conversion rate and growth for a few species. It includes some of my own published and unpublished results and

the results of an international group of scientists working on the energy budget of *Octopus vulgaris* (Wells, *et al.*, in press a,b,c). Finally, I shall try to summarize the present state of knowledge in these fields which currently is limited and rather patchy.

Material and Methods

Experiments were carried out principally on three species of the family Octopodidae easily obtained in the region surrounding Banyuls-sur-mer, France, namely: *Octopus vulgaris*, *Eledone moschata* and *E. cirrhosa*. *Eledone moschata* was reared from eggs laid in the laboratory to sexual maturity and spawning (see also Boletzky, 1975a). The other two species, having planktonic hatchlings, were collected by bottom trawls and reared from early benthic stages to spawning. Animals were kept either isolated or in small batches. In most experiments the octopods were fed crabs (*Carcinus mediterraneus*), but in some cases, different prey were offered, namely bivalves (*Mytilus galloprovincalis*, *Venus verrucosa*, *Tapes* spp.), gastropods (*Haliotis tuberculata*, *Patella coerulea*) and fish (*Sardina pilchardus*, *Engraulis* spp. and related species). Bivalves were provided for *O. vulgaris* based on shells collected beside occupied dens in the area of Banyuls-sur-mer (Ambrose, pers. comm.).

By way of comparison, rates for growth, daily feeding and food conversion (gross growth efficiency) were calculated according to Choe (1966):

$$\text{A. daily growth rate} = \frac{w_2 - w_1}{tW} \times 100$$

where w_1 is the initial wet body weight, w_2 the final weight, W the average weight, and t the numbers of days.

$$\text{B. food conversion rate} = \frac{w_2 - w_1}{FI} \times 100$$

where FI is the total food intake in grams of wet weight.

$$\text{C. feeding rate} = \frac{FI}{tW} \times 100$$

Results and Discussion

A. FOOD, FEEDING AND GROWTH

1. *Food preferences*

a. Food preferences in three species of Octopodidae in experimental work.

Given the choice of live crustaceans (mainly crabs), shelled molluscs or fish, *O. vulgaris*, *E. moschata* and *E. cirrhosa* from the Banyuls area invariably take the crabs and ignore the other food items at all growth stages. If no crabs are offered, the three octopods will accept molluscs and/or fish, but only after several days or weeks of starvation. Bivalves are preferred over gastropods. Bivalves are torn open or are killed by boring a hole in the shell and injecting poison from the posterior salivary glands. All animals fed over various periods of time on molluscs and/or fish, ignored these prey when crabs were co-offered and the crabs were devoured immediately. The preference for a crab diet in the laboratory was noted by Taki (1941) for *O. vulgaris* in Japanese waters and by Altman & Nixon (1970) in the Mediterranean.

Eledone cirrhosa from the North Sea feeds on a wide variety of crustaceans: crabs, shrimps and lobsters. Molluscs, when offered, were rarely accepted (Boyle & Knobloch, 1981).

b. Food preferences of *O. vulgaris* and *E. cirrhosa* in the sea.

Guerra (1978) analysed the stomach contents of *O. vulgaris* from the Catalonian Sea: 80% of the food consisted of crustaceans (27 species were identified), 12% were fish and 8% were cephalopods (3 species). Sanchez (1981a) found crustaceans to be the main food of *E. cirrhosa* in the same area, and Moriyasu (1981) who analysed the stomach contents of several hundred specimens of *E. cirrhosa* from the Northern coast of the Western Mediterranean, confirmed the observations of Sanchez. Moriyasu noted that although seasonal changes in the composition of the diet occurred, the main food organisms were crustaceans.

There are two studies on prey of *O. vulgaris* from the northwest African coast. Nigmatullin & Ostapenko (1976) analysed over 2000 stomach contents of animals caught at depths

ranging from 15 to 80 m. The diet consisted mainly of crustaceans (frequency: 61.5%; volume: 53.6%) followel by fish (29.5% and 25.5% respectively). Only 6.3% (9.5% in vol.) of the food was shelled molluscs and another 6.0% (7.5%) consisted of cephalopods, including the same species. Nigmatullin & Ostapenko indicated the percentage of crustaceans (mainly crabs) may be overestimated, since most octopuses came from day catches and since they consider crabs to be 'day time' prey whereas fish are taken mostly at night. According to Hatanaka (1979), gastropods and bivalves are the most important prey (45-60%), while fish, crustaceans and cephalopods account for 19-34%, 7-16% and 4-13% respectively. This author also noted that prey vary with time of the day and depth.

The southeastern African reef population of *O. vulgaris* investigated by Smale & Buchan (1981), preys mainly on the pelecypod, *Perna perna* which is extremely abundant in this area. In the western Atlantic, *O. vulgaris* also seems to feed primarily on shelled molluscs (Arnold & Arnold, 1969; Wodinsky, 1969; Hochberg & Couch, 1971).

As is typical of most *Octopus* species, *O. vulgaris* is an opportunistic predator. Analysing stomach contents is a tedious task, and the stomachs are often empty. However, stomach contents do yield valuable information on the food of a predator even though some food items may be digested faster than others and leave no trace, at least not identifiable ones.

Examination of the gastropod and bivalve shells found in the den of an *Octopus* may give good evidence of what an *Octopus* has eaten. However, octopuses are known to collect shells and stones to protect their dens, hence, the possibility remains that the shelled molluscs present around a den may not actually have been eaten by the owner of the den. On the other hand, crustacean remains are often carried away and leave no traces in den middens which may then lead to an overestimation of the mollusc prey. Stomach contents may mainly reveal the abundance of different prey, e.g. a pure mollusc diet if no crustaceans are available. However, food preferences do exist, at least under laboratory conditions, and they may well reflect a natural preference in the field. As far as *O. vulgaris* of the Catalonian Sea goes, there seems to be little doubt that crustaceans are the preferred prey.

c. General remarks on natural diets in Sepioids and Teuthoids.

To our knowledge, there is only one published analysis of the stomach contents of the nectobenthic cuttlefish, *Sepia officinalis.* The species accepts fish as readily as crustaceans, and molluscs, other than cephalopods, may occur in its diet as well as polychaetes (Najai & Ktari, 1979). The stomach contents of the benthic sepiolid *Rossia pacifica* consist mainly of crustaceans: about 80% (Brocco, 1970; Hochberg & Fields, 1980). The same holds for another member of the family, *Sepietta oweniana* (Summers & Bergström, 1983). For diets in captivity of the sepioids see Boletzky & Hanlon (this volume).

Slightly more is known of the diet of some loliginid and ommastephid species. In general, juveniles eat crustaceans while subadults and adults prey mainly on fish and squids. Worms (1979) was unable to find any crustaceans in the stomach contents of *Loligo vulgaris* of more than 100 mm mantle length. Macy (1982) showed very clearly the correlation between the size of *L. pealei* and the composition of its diet. He also showed that slight differences exist in this relationship between in- and offshore populations. Loukashkin (1976) and Karpov & Caillet (1978) analysed the stomach contents of *L. opalescens*, a key species in the food web of the pelagic and benthic communities along the coast of California. *Lolliguncula panamensis* exhibits a clear preference for fish diet (Squires & Barragan, 1979) as does the ommastrephid, *Ommastrephes bartrami* (Araya, this volume). An exhaustive list of food items for the squid *Illex illeceborsus* is given by O'Dor (1983). Besides crustaceans, fish and squids, *I. Illecebrosus* occasionally eats gastropods, pteropods and chaetognathes.

Several authors reported on the diet of the jumbo squid, *Dosidicus gigas*, a particularly voracious predator (Nesis, 1970, 1983; Hochberg & Fields, 1980; Erhardt *et al.*, this volume). Pelagic fish and squids seem to be the

main diet; small animals often feed on small crustaceans, subadults and adults prey heavily on the pelagic red crab, *Pleuroncodes planipes*. Pelagic molluscs also figure among the prey items. It should be noted that in some areas (Gulf of California), populations feed on small pelagic crustaceans during all stages of their life cycle, thus breaking the general pattern; an example of opportunistic feeding behaviour.

Mesopelagic oegopsids of small adult size (*Abralia*, *Abraliopsis*, *Pterygioteuthis*, *Pyroteuthis*) eat small crustaceans, mainly copepods, during their entire life cycle (Mangold, unpublished).

2. *Feeding rate*

It is well known that within the normal range of temperature adaptation of a species, higher temperatures lead to greater food intake, although exceptions occur among the cephalopods (Boletzky, 1975b). As an example for the rule, *O. vulgaris* fed *ad libitum* over several weeks ingested 40 to 83% of all crabs offered at 20°C, ate only 29 to 31% at 15°C, while those at 10°C ingested as little as 12 to 15% (Mangold & Boletzky, 1973). Accordingly, the daily growth rate varied between 1.14 and 5.08% at 20°C, between 0.69 and 2.74% at 15°C and between 0.35 and 1.42 at 10°C. Similar results were obtained with *E. moschata* (Mangold, 1983b), although the overall means at the three temperatures were lower for subadult animals than in *O. vulgaris*.

In *E. cirrhosa* and *O. salutii*, however, food intake was at its highest between 15 and 18°C and then decreased with increasing temperatures. Both species are adapted to cooler waters than *O. vulgaris* and *E. moschata* (Mangold & Boletzky, 1973; see also Boyle & Knobloch, 1982b).

The daily feeding rate for all four species of Octopodidae decreased with increasing size, a fact already known for *O. vulgaris* (Nixon, 1966) and many other species (Choe, 1966; Van Heukelem, 1976; Joll, 1977 and others) and recently confirmed by Boyle & Knobloch (1982b) for *E. cirrhosa*.

Food intake also depends on food availability and size at least in some species. Borer (1971 a, b) showed that doubling the number of prey for *O. briareus* and *O. bimaculoides* greatly increased food intake while reduction in food size decreased it. Food intake may also be dependent upon physiological limits such as the duration of the digestive processes (O'Dor *et al.*, 1980).

At least two other factors may influence food intake. One of them is the quality of food. When *O. vulgaris* of comparable initial size (300 to 350 g) were fed *ad libitum* over several weeks on either the crab (*Carcinus mediterraneus*), the limpet (*Patella coerulea*), the bivalve *Venus verrucosa* or the sardine (*Sardina pilchardus*), but otherwise maintained under strictly identical conditions (temperature rising from 10 to 13.5°C, normal day/night cycle), the mean feeding rate for animals fed on crabs was 3.6%, on limpets and *Venus* it was 2.5%, but on fish it was as low as 1.6%. These are preliminary results, based on wet weight relations. Further studies need to be conducted on a larger scale and also evaluated in terms of calorific values.

In the squid, *Illex illecebrosus*, however, the daily feeding rate was higher when fish (*Fundulus* spp.) rather than crustaceans (*Crangon* spp.) were offered *ad libitum* (Hirtle *et al.*, 1982). Although the squid ate a larger number of crustaceans, the total amount of food intake was higher with fish and the growth rate was higher on a fish diet. When the same quantities (weight) of fish or crustaceans were ingested, the daily growth rates were comparable. *Illex* seems to convert fish and crustaceans into cephalopod with a similar efficiency.

In many octopodid females, the amount of food ingested is drastically reduced or even stops altogether about 1 to 4 weeks before spawning. Growth may then stop rather abruptly and even may become negative. Brooding females of most species lose weight (Buckley, 1977, for *O. vulgaris*) although occasionally they may accept some food.

3. *Conversion rate*

While food intake is dependent upon temperature, food conversion or gross growth efficiency is not (Mangold & Boletzky, 1973; Van Heukelem, 1976; Pascual, 1978). Food conversion is also largely independent of the

size of the animals, but it appears to be lower in maturing individuals, especially in females of octopodid species. Mangold & Boletzky (1973) found that 20 to 80% (overall mean 55%) of the ingested food (crabs) was used for growth in *O. vulgaris*, whatever the temperature. More recent experiments gave slightly lower values, with an overall mean of 50% (Mangold, 1983a). In *E. moschata*, food conversion rate ranges between 18 and 70% (Mangold, 1983b) while in *E. cirrhosa* from the North Sea, the values lie between 10 and 70%, with an overall mean of 37% (Boyle & Knobloch, 1982b). These figures are very similar to those obtained for *E. cirrhosa* in the Mediterranean (Mangold, unpublished). In *O. cyanea* and *O. maya*, average food conversion rates are close to 40% (Van Heukelem, 1976). The overall mean for the small *O. joubini* was also found to be 40% (Forsythe, 1981; Forsythe & Hanlon, 1980), whereas in *O. tetricus* it is 47%, closer to the figures for *O. vulgaris* (Joll, 1977). It should be emphasised, however, that food conversion is highly variable, even with the same diet; not only between individuals of a species, but also on a temporal basis within individual octopuses (Mangold & Boletzky, 1973).

Preliminary results suggest that gross growth efficiency in *O. vulgaris* seems to be dependent upon food quality. When fed *ad libitum* on either crabs, sardines, limpets or clams, the food conversion averaged 50% when the food was crabs, a mainly proteic diet. In animals fed on sardines, a fatty diet, or on limpets or clams, relatively rich in carbohydrates, the conversion rates were distinctly lower about 25 and 20% respectively.

Smale & Buchan (1981) showed that in both males and females of *O. vulgaris*, conversion rates were higher when the animals were fed mussels (*Perna perna*) and rock lobsters (*Panulirus homarus*) than when fed on mussels only (males: 40.1 and 23.5%; females: 40.3 and 23.7% respectively).

Ingested food is used in two ways, for growth and for maintenance (the food required to keep an animal at a constant weight). Maintenance costs can be subdivided into energy used for standard metabolism, for specific organ activity (such as digestion and assimilation) and additional energy used in locomotory activity (Warren, 1971). The maintenance requirement decreases per unit body weight (Joll, 1977), it is dependent upon temperature, doubling or trebling with a rise of 10°C, and it is very likely to be higher in nectonic squids than in benthic octopuses (LaRoe, 1971; O'Dor *et al.*, 1980).

Gross growth efficiency in cephalopods is among the highest reported in the literature (Van Heukelem, 1976). On a wet weight basis, about 20 to 60% of the ingested food is used for growth. In *O. cyanea* and *O. maya*, gross growth efficiency is 40%; 55% of the ingested food is used in maintenance, only 5% (feces) is not absorbed (Van Heukelem, 1976). In *O. vulgaris*, the maintenance costs seem to be lower, about 45% on a crab diet, with 5% not absorbed. This difference, resulting in a higher gross growth efficiency (about 50%) may be simply due to the difference in temperature, since this species lives in cooler waters. It may also be due to a lower activity level. On an ashfree, caloric basis, the figures for conversion, maintenance and unabsorbed food for *O. cyanea* on a crab diet are 60, 36 and 4% respectively (Van Heukelem, 1976).

Wells *et al.* (1983, a,b,c) established the metabolic costs in *O. vulgaris* by measuring oxygen consumption. The standard metabolic rate in starving, inactive animals of 300 to 400 g at 21-22°C is about 56 ml $O_2\ Kg^{-1}\ h^{-1}$. The 'routine' metabolism (mean values from starved resting and active animals and from fed resting animals, $n = 341$) is 75 ml $O_2\ Kg^{-1}\ h^{-1}$. Feeding raises the metabolism in two ways. The capture, ingestion, digestion and assimilation of a prey (crab) causes an increase in oxygen uptake that lasts about 6 hours and peaks during the 1st to 3rd h after capture. This short-term (6 h) cost of assimilating the 10 to 12 g of flesh from a 20 g crab is in the order of 9 ml $O_2\ g^{-1}$. There is also a long-term effect of feeding. Feeding a starved octopus in the 300 to 500 g size range a 20 g crab each day results in a progressive rise in oxygen consumption over the first 2 to 4 days following the first meal. Small animals do treble their oxygen uptake, larger ones double it. After these 2 to 4 days, the oxygen consumption decreases a little or remains steady. The size of the meal greatly affects oxygen consump-

tion. While very small meals (less than a 10 g crab for an octopus of 300 to 500 g) causes only a slight increase, very large meals (several crabs of 20 to 30 g each) produce a very large increase, both in the short and the long term. After several days of heavy feeding, following a starvation period, the animals cut down their food intake (Mangold, unpublished; Wells *et al.*, 1983, c). Compared to the costs of feeding, the costs of locomotion in this rather inactive species are low, although they are high per hour: 253 ml O_2 Kg^{-1} Km^{-1} for an octopus of 500 g travelling at 22°C at 0.34 Km h^{-1} (Wells *et al.*, 1983, a,b). Feeding is definitely the most important factor that determines the daily energy requirement in this species (Wells *et al.*, 1983, c).

O'Dor *et al.* (1980) observed that captive *Illex illecebrosus* which had ingested a large meal, more than 20% of their own body size, refused to eat the next day. Meals of about 10% body weight were regularly accepted.

The same authors (1980) compared values for feeding rates, growth rates and conversion efficiency of *I. illecebrosus* with the corresponding values from *O. vulgaris* for animals of the same size range and at comparable temperatures. Growth, in *Illex*, is slightly faster, but the conversion rate is lower. Squids have to eat about twice as much as an octopus. The low conversion rate is partly due to the higher activity of the squid, hence higher maintenance costs, but it may also depend on the quality of food which was fish (*Fundulus*) for *Illex* and crabs (*Carcinus*) for *Octopus* (but see Hirtle *et al.*, 1982).

4. *Growth*

Data on growth are available from two sources, field and laboratory studies, the former mostly carried out during fishery surveys for commercially important species. For convenience, in field studies, growth is usually expressed as increase in length, the standard measurement being the dorsal mantle length. In laboratory studies, growth in decapod cephalopods is mostly measured in terms of increase in length while for octopods, weight measurements prevail. In both types of studies few authors record growth by indicating both length and weight (Boletzky, 1975a; Hanlon, 1975; Opresko & Thomas, 1975; Forsythe, 1981, for octopods; Richard, 1971; Hixon, 1980; Amaratunga, 1980, for decapods).

The difference in shape of the growth curves for length and weight measurements depends upon the body proportions, especially the development of the arm apparatus in many octopodid species (see Forsythe, 1981).

In field studies, growth and age can only be accurately correlated when there is clear evidence that a single year class from a stable population is under study, an almost ideal situation. In species where the spawning season is prolonged or extends throughout the year, this may prove to be an impossible task (see Mangold & Boletzky, 1973). Field growth studies are also biased by the sampling methods, e.g. the lack of postembryonic and juvenile stages in the catches.

In laboratory studies, growth and age can be linked only when the actual ages of the animals are known (i.e., those species reared from hatching onwards). All these species have large eggs and benthic young (Boletzky & Hanlon, this volume) with the exception of one species with planktonic hatchlings, *Loligo opalescens*, which was successfully reared from hatching to spawning in Galveston (Yang *et al.*, 1980, 1983 and Hanlon, pers. comm.). For species reared from wild-caught stages onward, the growth over a given period of time can be accurately determined, but the link with age remains approximate.

As reported in the above sections on feeding and conversion rates, growth is determined by many factors. High variability makes it almost impossible to compare controlled laboratory growth with growth in natural populations. Many cephalopods do not live in the same habitat (e.g. depth) or area during their whole life cycle. A number of species migrate to stay in similar temperature regimes, while others, very clearly, encounter different temperatures during their life time, e.g. those that live in shallow temperate waters where differences in temperature between summer and winter affect their daily food intake as well as their metabolic costs.

Levels of activity may be different in wild and

captive animals, especially in nektonic species, and this certainly influences their metabolism.

Food is overabundant in most laboratory experiments (but see Boletzky, 1974b, 1979) whereas in the sea animals may not experience such ideal conditions on a sustained basis. If the growth pattern within a population of a species is different from that of individuals of the same species obtained in the laboratory, it may not be possible to determine which factors are responsible for the difference.

O'Dor, *et al.* (1980) found that growth rates of field populations of *I. illecebrosus* are well below those in animals maintained in the laboratory. The authors estimated that the activity level of the captive animals kept in a large pool was probably comparable to that of field animals (temperatures were approximately the same), and they concluded that food intake must account for the difference. It seems, indeed, that the population does not feed *ad libitum* during late summer and autumn because its main prey, capelin (*Mallotus villosus*), and other fish species, are scarce. Hixon (1980) also found that the growth rate in three species of loliginid squid, *Loligo pealei*, *L. plei* and *Lolliguncula brevis* in the Gulf of Mexico was distinctly higher when calculated from laboratory results than from field data.

However, for other species, such as *E. cirrhosa* in the North Sea, *O. cyanea* in Hawaii and *O. vulgaris* in the Catalonian Sea, growth rates of animals reared in the laboratory are comparable to those of wild animals (Boyle & Knobloch, 1982b; Van Heukelem, 1976; Mangold, 1983a).

A variety of different growth models have been proposed for cephalopods. Figure 1 illustrates 5 growth curves which have been applied to loliginid species only: (A) linear growth (*L. opalescens*, Fields, 1965); (B) asymptotic growth or von Bertalanffy type curve (*L. pealei*, Verrill, 1881); (C) cyclic growth (*L. vulgaris*, Tinbergen & Verwey, 1945); and (D) exponential growth (*L. vulgaris*, Mangold-Wirz, 1963; and *L. pealei*, Summers, 1971). The first four curves are based on data obtained from field populations. The fifth type (E) represents sigmoidal growth for *L. pealei*, *L. plei* and *Lolliguncula brevis* obtained from laboratory

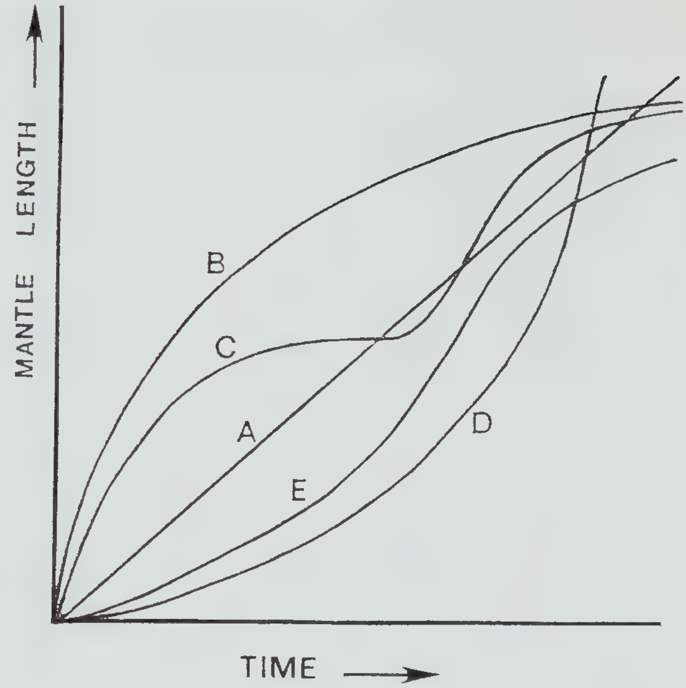

Figure 1. Growth curves for five loliginid species (after Hixon, 1980). A = linear growth (*Loligo opalescens*, Fields, 1965), B = asymptotic growth (*L. pealei*, Verrill, 1881), C = cyclic growth (*L. vulgaris*, Tinbergen & Verwey, 1945), D = exponential growth (*L. vulgaris*, Mangold-Wirz, 1963; *L. pealei*, Summers, 1971), E = sigmoid growth (*L. pealei*, *L. plei*, *Lolliguncula brevis*, Hixon, 1980).

data (Hixon, 1980). The growth curve for *L. opalescens* reared in the laboratory is exponential (Yang *et al.*, 1980). Thus, for a given species, growth curves are different not only when laboratory and field studies are compared, but also when animals of the same species from different areas are compared.

However, most field data for octopods as well as for teuthoids fit a von Bertalanffy type curve (e.g. for *O. vulgaris*: Guerra, 1979; Pereiro & Bravo de Laguna, 1979; and Hatanaka, 1979; for *I. illecebrosus: Squires, 1967; and Amaratunga, 1980; and for I. coindetii*: Sanchez 1981b). According to Hixon (1980), this model probably does not account for growth of very young planktonic stages. A cyclic growth pattern probably occurs in species with a two year life span which live in waters with large temperature fluctuations, as e.g. *L. vulgaris* in the North Sea (Tinbergen & Verwey,

1945). A sigmoidal growth curve is proposed by Hixon (1980) for loliginid species of short life span wherein the initial exponential growth is slowed down by the onset of sexual maturation which means, in terms of a population, when about 50% of the animals are mature. Richard (1971) reared *Sepia officinalis* at different temperatures and showed that the growth curve was always sigmoid, the inflection point varying with the temperature: 70 to 90 days at 25°C; 100 to 120 days at 20°C and 200 to 250 days at 15°C.

Cephalopods grow until they reach sexual maturity at which point growth stops or even declines. Therefore, it is arguable that growth is non-asymptotic. Following this line, Van Heukelem (1976) ruled out any equation which incorporates an asymptotic weight factor when studying the growth of *O. cyanea* and *O. maya*. The author found that the early growth phase is best represented by the exponential equation:

$$W_2 = W_1^{e\,kt}$$

where W_2 and W_1 are the final and the initial weights, T the time and k the instantaneous coefficient of growth. This exponential growth phase is very fast. The following phase which lasts more or less to sexual maturity is slower and best fitted by the equation:

$$W = ax^b$$

where a is the elevation, b the slope and x the age in days. This phase is called the logarithmic growth phase (straight line on a double log paper). Forsythe (1981) found the same growth pattern in *O. joubini* and pointed out the striking similarity in growth patterns for octopodid species of different life spans and very different adult sizes (Table 1).

Boyle & Knobloch (1982b) constructed an ideal curve for *E. cirrhosa* from the North Sea for maximum growth rates from 10 to 1000 g, and this curve best fits the parabolic model. This model takes into account the relative slow growth in animals freshly brought from the sea and the decline in growth at sexual maturity.

We are thus confronted with at least half a dozen growth models. They may reflect real differences in growth patterns of different cephalopod species, or they may be biased by sampling methods (field studies) and the high adaptability of cephalopods to artificial laboratory conditions. The ability to rear species of all suborders, regardless of whether the young animals are benthic or planktonic may clear up this rather confusing picture. Indeed, laboratory experiments provide the raw material for such theoretical considerations. However, one must be extremely careful when trying to apply a model to natural populations. One of the main questions will be whether size

TABLE 1

Growth patterns of octopuses relative to size at spawning and life span.

Species	Size at spawning g	Life-span months	Authors*
O. joubini	20-30	5.5-6.5	Forsythe, 1981
O. briareus	500-1500	12	Hanlon, pers. comm.
O. vulgaris	500-3000 mean 1500	15-18	Mangold, 1983a
O. maya	700-6500 mean 3200	10	Van Heukelem, 1976
O. cyanea	700-6500 mean 3600	12-15†	Van Heukelem, 1976
E. moschata	250- 600 mean 400	15-18	Mangold, 1983b

* The authors quoted are those who described the 'exponential-logarithmic' growth pattern for 6 species. The size at spawning and the life-span have been indicated by other authors.
† From settlement.

classes in wild and reared populations can be compared with respect to their age structure.

B. FEEDING BEHAVIOUR AND SEXUAL MATURATION

It is well known that the females of many species of Octopodidae slow down their food intake several days or weeks before spawning (for a review see Wodinsky, 1978). There seems to exist a kind of 'interaction' between feeding behaviour, hence growth, and sexual maturation, or 'maturation versus somatic growth' as O'Dor & Wells (1978) put it.

As an example: I reared *E. moschata* from hatching to spawning. Animals that hatched over a period of 3 days from an egg mass laid by a single female were selected. Very early growth differed only slightly when the animals, fed *ad libitum*, were kept isolated. In animals that shared a tank, weight differences at the age of two months were 10 fold or higher (Mangold, 1983b), perhaps as the result of the establishment of a feeding hierarchy (see also O'Dor *et al.*, 1980, for *I. illecebrosus*). Table 2 shows the minimum and maximum weights for 10 animals kept isolated and for 10 animals that shared a 60×40×20 cm plexiglass tank provided with an adequate number of shelters.

It should be emphasized that even with isolated animals, the period of heavy feeding and rapid growth, was variable, as were the sizes and the ages at which sexual maturity was attained. Some females stopped eating at the age of 7.5 to 8 months and these, mostly of relatively small size, were the first to spawn. Others continued to feed intensively and spawned at a larger size and a greater age, 10 to 12 months (Mangold, 1983b).

In earlier experiments with wild-caught *E. cirrhosa* several animals of similar initial size were reared in the same tank (Mangold & Boucher-Rodoni, 1973). The number of crabs offered was twice the number of *Eledone*. They were apparently competing for food. After 3.5 months, the smallest animal which had eaten less than the others, was the first to spawn; the largest *Eledone* matured 3 months later.

One could argue, of course, that the wild-caught *E. cirrhosa* were of unknown age and of unknown feeding history, and that in spite of their similar initial size, they were in fact of different age. This was certainly not true in the *E. moschata* experiments where both, age and feeding history were precisely known.

Field observations demonstrate that enlargement of the ovary may occur over a wide range of body sizes. There is no simple relationship between body weight and ovary weight or stage of maturity of the eggs. In males, the relationship between body weight and gonad weight is distinctly closer, at least in the three octopodid species studied: *O. vulgaris, E. cirrhosa* and *E. moschata* (Table 3). Thus, females of these three species become mature in the field at different sizes and very likely also at different ages. Several parameters are thought to influence the process of sexual maturation in cephalopods, namely light, temperature and food availability at different stages of the life cycle (Richard, 1971; Van Heukelem, 1976; Mangold, 1983a). Combined effects of these parameters can result in producing mature females at different sizes and ages.

But why do females hatched within 3 days of each other, from eggs laid by a single female, become mature at different sizes and ages when reared under strictly identical conditions as in my *E. moschata* experiments (Mangold, 1983b)? Several authors have noticed that females in captivity tend to mature precociously

TABLE 2

Minimum and maximum weights in grams attained by 10 isolated and 10 cohabitant specimens of *Eledone moschata* reared from hatching to 60 days.

Day	1	15	30	45	60
isolated	0.3	0.96-1.06	2.15-2.45	4.81-5.32	9.50-10.52
sharing a tank	0.3	0.41-2.00	0.51-3.72	0.65-8.03	0.98-17.85

TABLE 3

Relationship between body weight and gonad weight, r, in males and females of *Octopus vulgaris*, *Eledone cirrhosa*, and *E. moschata*.

Species	*n*	*r*	Area	Authors
O. vulgaris				
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females	286	0.560		
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(Wells, 1978; Boyle & Knobloch, 1982b). This seems to be true for *E. moschata* as far as size is concerned; the mean size at spawning is smaller in captivity than in the field (Mangold, 1983b). But this still does not answer the above question, and I have no answer to offer at the present time.

What *is* known is that the feeding behaviour changes with the approach of sexual maturity when females begin to eat less and less regularly. Wodinsky (1978) showed that mature and brooding females of *O. vulgaris* along the east coast of America not only eat less, they also switch from boring holes into the shells of gastropods to pulling the prey out by force. According to this author, the production of the toxic secretion of the posterior salivary glands may be inhibited.

Concluding remarks

Cephalopods are voracious predators that feed on a wide variety of live prey. Food size spans a wide range from very small planktonic animals to prey equal or even larger in size to that of the predator. This general statement is based on stomach content analysis, feeding studies in rearing and maintenance experiments of about 50 species (Boletzky & Hanlon, this volume and personal observations). The most important food is crustaceans of all kinds, pelagic as well as benthic. Almost no information is available on the prey of the 650 or more other cephalopod species known to exist, many of which are themselves important prey for marine mammals, birds and fish (Clarke, 1977, 1980). There is a serious lack in our knowledge as pointed out by Clarke (this volume). Not only should we know what cephalopods eat during their entire life cycle, we also have to know what the different food organisms represent in terms of caloric values.

Most species change food habits with growth. *Octopus* species often switch from small crustaceans to larger ones, while others eat small crustaceans during the whole life span (e.g. *O. cyanea*, Van Heukelem, 1976), still others may change food species as well. Squids usually feed on crustaceans in early stages whereas fish and fellow squids or other cephalopods are preferred later. However, some species do not conform to this general pattern. Food may vary with distribution and depth (inshore/offshore) rather than with size, as reported for *L. opalescens* by Karpov & Caillet (1978).

Food intake is dependent upon temperature, size of the predator (and prey), number of prey, quality of food; feeding behaviour changes in many octopodid females as sexual maturity approaches. Young octopuses eat as much as 10 to 20% of their own body weight per day; during this phase, their daily growth rate averages 6% (Van Heukelem, 1976; Forsythe, 1981; Mangold, 1983a,c and others). This high food intake corresponds to the first very fast (exponen-

ial) growth phase. Food intake and growth rate drop during the second (logarithmic) phase to about 5% and 2% respectively, and both slow down drastically with sexual maturity. Food intake in squids may be as high as 50% or higher in very early stages (Hurley, 1976, for *L. opalescens*) whereas in subadults and adults, it varies between 10 and 25% (LaRoe, 1971; Hanlon, 1978; O'Dor *et al.*, 1980; Hirtle *et al.*, 1982). The higher food intake in squids probably is related to higher metabolic costs associated with their higher activity.

Gross growth efficiency or food conversion in cephalopods is among the highest of all animals reported in the literature.

Growth in reared or cultured cephalopods may or may not follow a unique pattern. However, since growth is dependent upon many factors that are likely to vary in nature and to be different from the controlled environmental conditions in the laboratory, the application of a laboratory model to field population dynamics must be handled with great caution and can probably never be assured with certainty.

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No attempt has been made in this paper to compare the state of the art on food, feeding and growth in cephalopods with that in fish, their primary competitors. Such a comparison would have demonstrated the enormous gaps in our knowledge of cephalopods. Only within the last two decades has the scientific community recognized the role of cephalopods in the food web of the oceans, their importance as a high quality protein resource for human consumption and their uniqueness as a research model. It is now the common task of basic and applied research to fill the gaps.

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CEPHALOPOD BIOMASS – ESTIMATION FROM PREDATION

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Abstract

North Atlantic deep sea cephalopods caught in research nets (mouth opening of 9 m^2) and large commercial trawls are compared with those eaten by Sperm Whales. It is shown that at three latitudes the nets and whales sample cephalopods very differently. Research nets are biased towards collecting small species and young specimens of several families, principally gonatids, cranchiids, enoploteuthids and onychoteuthids, while sperm whales are biased towards catching much larger cephalopods, particularly histioteuthids. Commercial trawls tend to bridge the gap in size of cephalopods selected by research nets and whales but where comparisons are possible they have a bias towards catching enoploteuthids. The contribution by numbers and weight of different cephalopod families to the cephalopod fraction of the diet of sperm whales throughout the world is reviewed.

A detailed study of Antarctic cephalopods in the diet of large predators including cetaceans, seals and birds indicates areas where more knowledge is required to make accurate estimates of the biomass of Antarctic cephalopods consumed. The value of direct studies of food webs for quantitative consideration of particular cephalopod taxa is demonstrated and discussed.

Introduction

Commercial catches of cephalopods have increased over several decades and an increasing number of species are now utilised for human consumption. The species concerned live in or move into inshore shallow seas at some stage of their life. We know that many other species live in the deep seas and are not caught commercially. Many of these may not be as highly nutritious as the inshore species and, up to the present, fishing techniques have not been adapted for their capture but their future exploitation cannot be ruled out. While this alone warrants their further investigation the fact that they are a principal food of many cetaceans, seals, fishes and birds shows that a proper understanding of oceanic ecology would be unobtainable without studying the cephalopod fraction by every means available.

The direct approach to understanding the importance of cephalopods in marine food webs is to examine stomachs of their common predators and to examine the stomachs of the cephalopods taken as prey. This approach has advantages: (1) the information provided is directly relevant to the food web, (2) effort is not wasted on ecologically 'unimportant' species (i.e. species which are both rare and small) and, (3) it is not necessary to know the sampling bias of predators (as opposed to research nets), since the total stock from which the cephalopods are being removed need not be calculated for many ecological purposes (large changes in stock, however, should be reflected by changes in the predators' diet). This direct approach also presents problems, but, because cephalopods are so poorly sampled by nets in the open ocean, it is the only approach at present which promises to provide answers to many of the questions of food web ecology.

The aim of this paper is to examine the difficulties and advantages of this direct approach and, in particular, to suggest ways of removing the barriers to a more quantitative study of cephalopods as important members of a food web.

Nets and Predators as Samplers

Even the largest nets, unless they are used on the bottom in less than 200 m of water, seldom catch cephalopods longer than half a metre. But such shallow water represents only a very small percentage of the sea's surface area and volume, and therefore does not harbour the full range of cephalopod species, especially the larger squids. Many of these are in the midwaters, that stretch down more than 2 000 m from the sea surface and across 70% of the earth's surface. Here we can sample only with midwater nets and hooks and lines. Such methods would lead us to suppose that in most regions cephalopods more than a half metre long are extremely rare. Can we believe this or should we doubt the efficiency of our methods?

If our methods are inefficient, how can we test them and how can we find a remedy?

To know if large cephalopods are common in the ocean is crucial to an understanding of the food webs and the biomass of the sea because, if they are, they will consume a significant fraction of other organisms and will themselves provide a large reservoir of food for fishes, whales, etc. The components of the web itself should answer the question 'Are large and poorly-known cephalopods important in the sea?'; the study of one large cephalopod predator should be enough to give an indication. The Sperm Whale is admirable for this purpose because: (1) it eats cephalopods primarily; (2) it is large and thus eats many large cephalopods; (3) it is abundant with a population estimated at one to two million individuals; (4) it is world ranging and has been killed commercially in many parts of the world. While this whale is an efficient sampler, gastric juices quickly dissolve and distort most of the cephalopod flesh. However, thousands of horny cephalopod mandibles or beaks remain undigested. An average of 2 000 and up to 8 000 cephalopods are represented in each Sperm Whale stomach. Most lower beaks can be identified to family, genus and often species and this provides our key for comparison with net hauls.

How do the data based on beaks from Sperm Whale stomachs compare with data from nets used in the deep sea? Precise scientific comparison is not possible because of differences in area, depth, time of fishing, etc. However, a broad comparison *is* possible and is valid because (1) the quantity of cephalopods caught by research nets does not vary enormously wherever they are used in the deep sea, (2) the number of lower beaks from Sperm Whales examined to date (>150 000) probably about equals the total number of net-caught deep sea cephalopods ever identified, and (3) the information from the two sources is so different that there is little possibility that differences are due only to chance or to difference in habitat sampled.

Comparisons have been made between beaks from various predators and net-caught cephalopods from many parts of the world but, as an example, we will consider North Atlantic data. Let us compare the cephalopods caught in almost 600 hauls made with the commonly used rectangular midwater trawl (Baker *et al.*, 1973; Clarke, 1977; Clarke & Lu, 1974, 1975; Lu & Clarke, 1975a & b) with those caught by 42 large commercial Engels and British Columbia trawls used over great depths (Clarke, 1977; Clarke & Lu, 1974), and the beaks from Sperm Whales caught commercially off Iceland, Spain and Madeira (Clarke, 1962; Clarke & MacLeod, 1974, 1976).

First we should consider the overall numbers collected in various ways. The only two complete stomach contents from the North Atlantic contained 2 136 and 3 776 lower beaks. The total number of cephalopods taken by over 400 research nets (mouth area = 9 m²) was 4 041 or about 10 per net. Thirty-four hauls with an Engel's midwater trawl (mouth area: 35×20 m $\simeq$ 700 m²) used between 28-38°N, 8-20°W averaged 58 cephalopods per haul and 8 hauls with a British Columbia midwater trawl (mouth 15×15 m $\simeq$ 230 m²) averaged 50 cephalopods per haul. To catch 3 000 cephalopods the 9 m² nets would have to be fished successfully for at least 50 days and the large trawls for more than 10 days. Secondly, we might ask if data derived from whales give the same information as that derived from nets or whether the biases in sampling give totally different results. Figure 1 compares the percentages of the most abundant families in the three sets of samples. Clearly the histioteuthids are dominant in the whale samples while the commercial trawls predominantly catch enoploteuthids at 30° & 40°N. Cranchiids are important in the 9 m² nets (21-28%) and in the whales caught in cold water off Iceland. Otherwise, the 9 m² net catches vary considerably with latitude taking mainly gonatids in high latitudes and several other families in lower latitudes.

But what of the size of cephalopods sampled? Figure 2 shows the mantle length of the largest squid by family caught in the 9 m² research nets and the minimum and range of mantle lengths of squids found intact in stomachs of sperm whales caught throughout the world. Except for the cranchiids and histioteuthids the ranges do not overlap. In

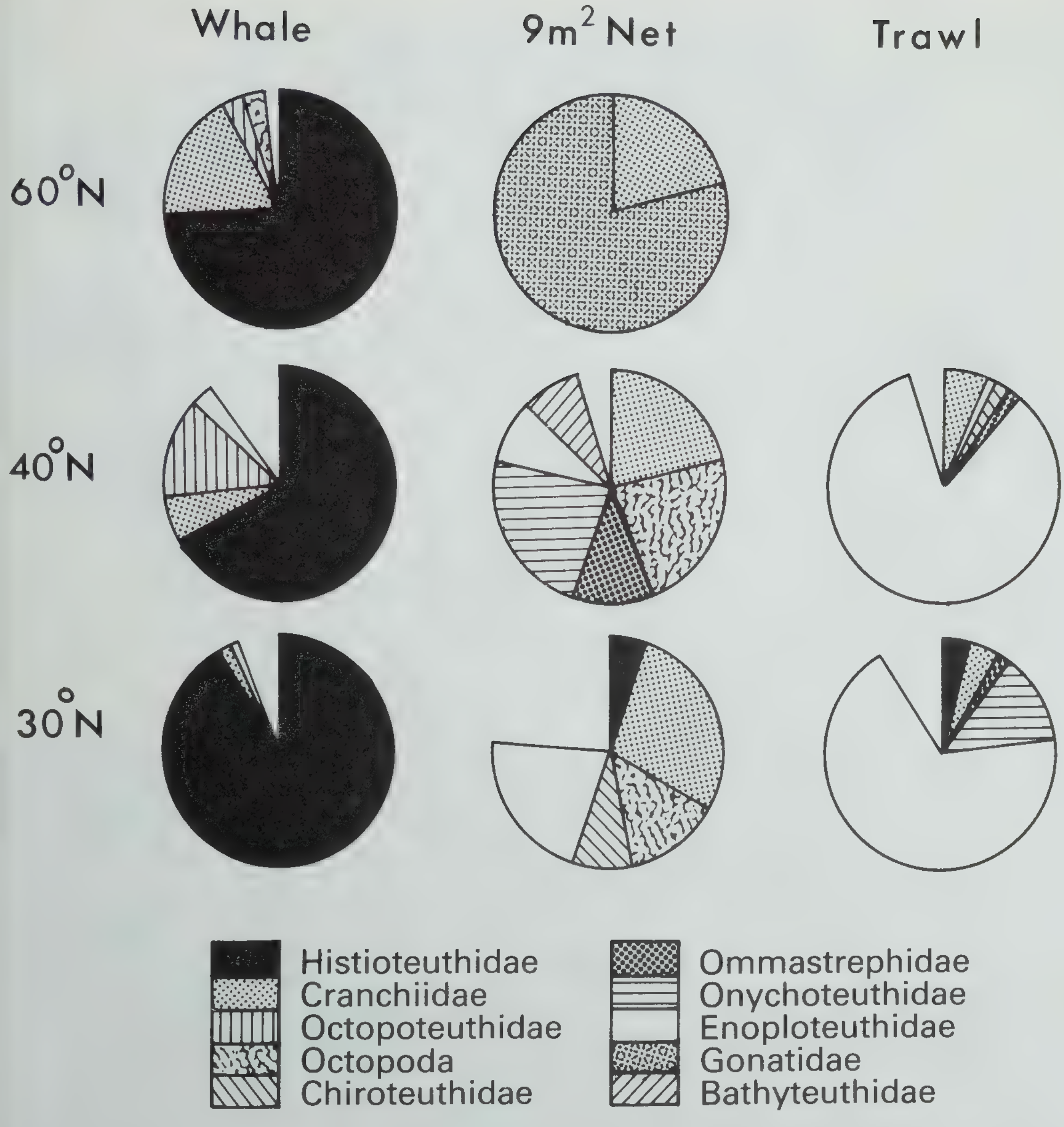

Figure 1. The families of oceanic cephalopods (mainly squid) caught by Sperm Whales, research nets ($9\ m^2$ mouth opening) and commercial trawls in three areas of the North Atlantic. The whales eat histioteuthids, cranchiids and octopoteuthids primarily. Nets catch squids mostly from other families.

fact, some squid *beaks* from whale stomachs are more than 10 cm long and exceed the maximum *mantle length* of squids from all but two of the families from nets! Squids from commercial trawls often are larger than those from $9\ m^2$ nets and a few ommastrephids from these also exceed the minimum length of those from sperm whales.

Thus, comparisons between families show that research trawls, commercial trawls and whales all provide different and complementary views of cephalopod abundance, size and distribution.

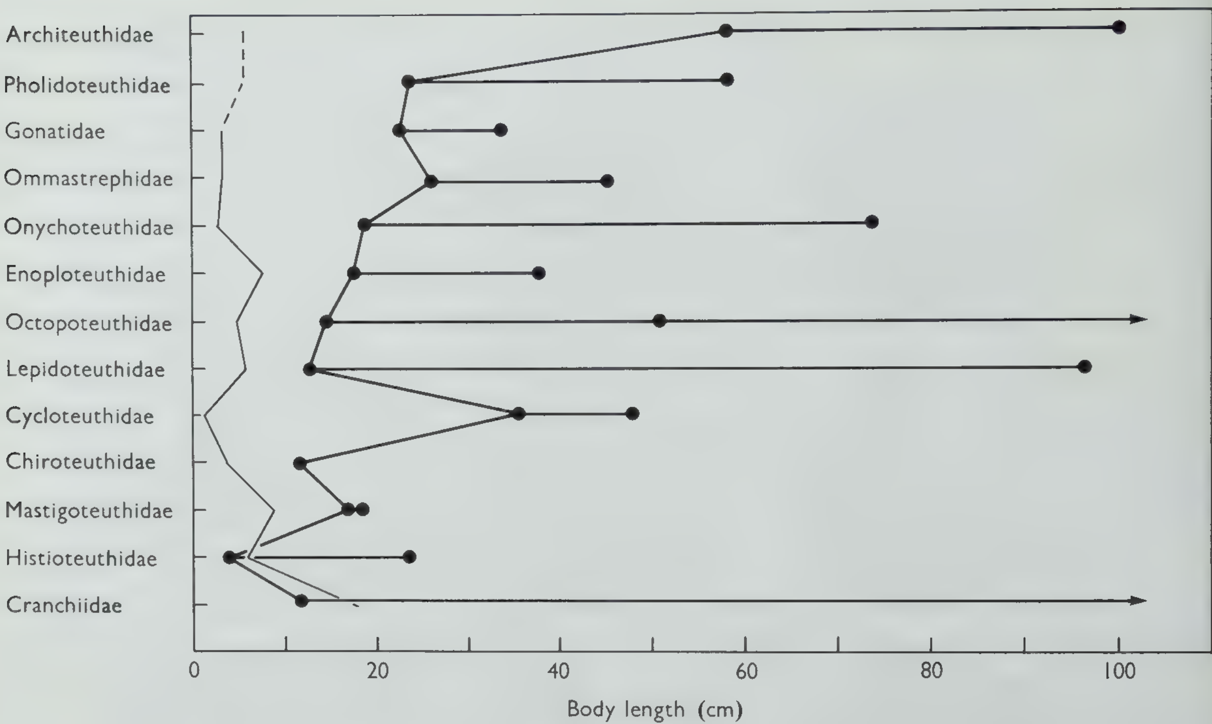

Figure 2. The mantle lengths of squids of various families caught in nets and by Sperm Whales. The range of sizes found in Sperm Whale stomachs is shown by a horizontal line for each family; the lower ends of the ranges are connected by a heavy line. A thin line joins the maximum mantle length for squids of each family caught in 600 research net hauls (9 m² mouth).

A CONSIDERATION OF THE OCEANS WORLDWIDE

An analysis of beaks taken from Sperm Whale stomachs shows the important families in the diet of sperm whales throughout the world (Fig. 3, top). In temperate regions and Iceland, histioteuthids are very dominant (30-91%) except in the North Pacific where they form a small (<8%) part of the diet. In most temperate regions, except the North Atlantic and North Pacific, the octopoteuthids also are well represented (10-33%). Whales in the North Pacific have large proportions of gonatids (32-69%; also common in high latitude Atlantic nets), onychoteuthids (3-24%) and cranchiids (26-33%). From the beaks (Fig. 3) the onychoteuthids and cranchiids are the main groups in the Antarctic with 53% and 23% respectively. Finally, Peru and some North Pacific samples differ from all the rest by having appreciable numbers (16-17%) of another family, the Chiroteuthidae.

It is possible to estimate mantle length and weight of squids in different families by measuring beaks. Figure 3 (bottom) shows that, by weight, histioteuthids are still important but they are less dominant in the diet than octopoteuthids off Spain, South Africa and Australia. In the Tasman Sea and off Madeira the architeuthids are sufficiently large to be important in the diet (19% and 40% respectively) while various families particularly the ommastrephids, enoploteuthids and pholidoteuthids are moderately important by weight in some regions of the southern temperate seas. In the Antarctic, a gigantic cranchiid growing to over 10 m total length and, except for a few larval specimens, only once caught by a net, forms the bulk (76%) of the sperm whale's food. Second to this are the onychoteuthids (21%) which also comprise most of the food by weight in the eastern North Pacific. The weights

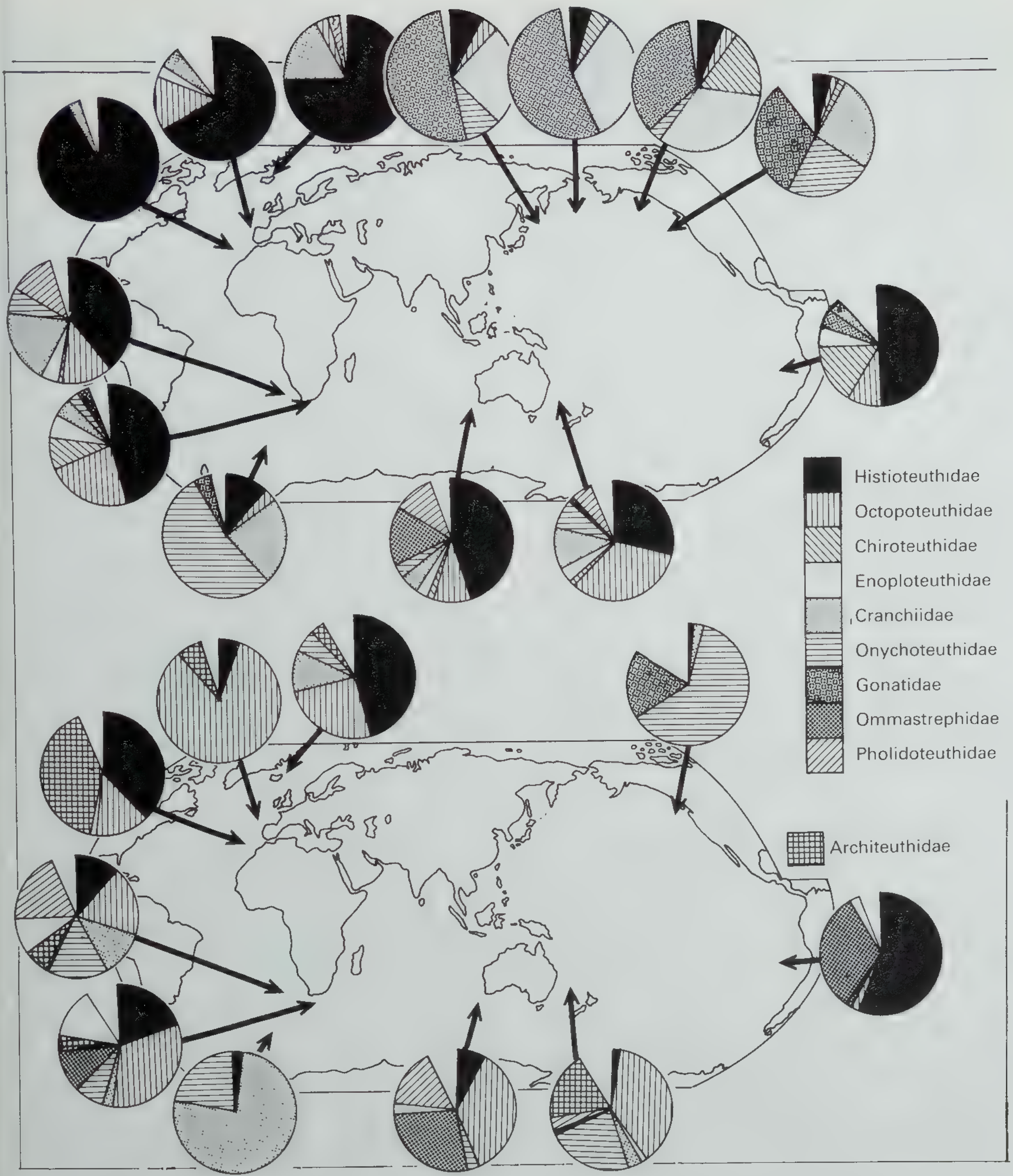

Figure 3. Squid families in the diet of Sperm Whales caught in various regions of the world. Top, Composition based on the number of lower beaks. Bottom, Composition by weight estimated from the numbers and sizes of beaks. Data for Kurile islands, Aleutian islands and Gulf of Alaska from Tarasevich, 1963, 1968. Other data from papers by Clarke and colleagues.

of flesh of cephalopods from Sperm Whales caught off Japan (Okutani *et al.*, 1976; Okutani & Satake, 1978; Kawakami, 1980) show that histioteuthids are most important by weight in that region (30-38%) with unidentified squids providing 27% of the cephalopod weight (these conclusions are biased by differential digestion, are not readily comparable with beak studies and have therefore not been included in fig. 3).

The mean weight for individual squids represented by beaks taken from whales in various parts of the world varies from 0.6 to 8.0 kg. From research nets deep sea squids average less than 0.002 kg in weight, and from commercial midwater trawls less than 0.1 kg.

To determine what food resources are available to man and what effect on these resources the removal of other resources will have, the biologist must estimate the biomass of all the important groups in the sea and he must understand the interactions between animal groups. Fisheries exploitation has brought us knowledge of the important organisms contributing to the total biomass of the continental shelf regions. Very much less is known of the biosphere of the deep oceans, and it is clear from the differences between net catches and samples from sperm whales that calculations of biomass of squid based on nets used so far will give grossly inaccurate estimates. The basic data required by the biologist estimating biomass are the numbers and weights of the different types (be they species, genera or families) that occur in a specified volume of water. If we cannot determine this for cephalopods from nets, can samples from sperm whales help? Using estimates of the whale population size, food consumption and average body weight, the weight of squid consumed per year is well over 100 million tonnes (Clarke, 1977, 1980). This figure compares with about 70 million tonnes for the total world annual catch of fishes and probably exceeds half the total biomass of man himself. If this is the weight consumed by sperm whales, what is the total weight of squids in the world? We can only guess.

Many oceanic animals eat squids including toothed whales, dolphins and porpoises, seals, birds such as albatrosses and penguins and fishes such as tunas and sharks. Some eat the same species as the sperm whale while others eat a very different combination of species, often quite different from that sampled by nets. We hope to somehow sum the estimates from all the different 'views' to obtain an idea of the populations and biomass of cephalopods in the world or in any particular area.

CEPHALOPODS OF ONE OCEAN – THE ANTARCTIC

If we are to use the study of predators' food to determine cephalopod numbers and biomass in the world we need much more information on the deep sea fauna than we have at present. One way to assess the problem is to study a restricted geographical area where information can be gathered from a variety of predators whose distribution, numbers and biology are available. However, boundaries circumscribing sea areas and their faunas often are not distinct or well known. An exception is the Antarctic Ocean, which is well defined by the Antarctic continent to the South and the Antarctic Convergence to the North. Apart from its distinct boundaries this ocean has two further advantages for study: it contains fewer species than warmer oceans and recent interest in krill stocks has led to much activity by ecologists in the region. If any oceanic area can be used to assess the feasibility of a cephalopod study based on their predators it is the Antarctic Ocean. That is not to say that all information is available to fulfil the task, but it should be sufficient to establish the missing factors in our formula for estimating the biomass of cephalopods of the region.

The predators of cephalopods in the Antarctic Ocean include whales, seals, birds and fishes. The following cetaceans are common in the Antarctic Ocean and include squids as an important part of their diets; *Mesoplodon layardii* (Straptooth Beaked Whale), *Cephalorhynchus commersonii* (Commerson's Piebald Dolphin) and *Lissodelphis peronii* (Southern Rightwhale Dolphin). Others eating some cephalopods are *Lagenorhynchus australis* (Blackchin Dolphin), *Hyperoodon planiformis* (Southern Bottlenose Whale), *Berardius arnuxii* (Southern Fourtooth Whale) and *Orcinus orca* (Killer Whale). The numbers and biomass of

these cetacea and the proportion of their diet comprising cephalopods is not known. However, there is little doubt because of its size that the Sperm Whale (*Physeter catodon*) is the main odontocete predator of squids (Table 1). This whale eats few fishes in the Antarctic—less than 5% of the diet. Only adult males migrate into the Antarctic Ocean and Laws (1977) accepted that one-third of the exploitable male population of the Southern Hemisphere spends the summer there. I have taken the initial stock (i.e. before whaling) as a basis for this calculation and have derived the biomass of each of the genera of squid from the estimated total weight of squids eaten (Table 2). The weakest factor in the calculation is the Sperm Whale stock estimate for the Antarctic and the assumption that one-third are present only in the summer. I have taken the mean weight of the whales as 40 tonnes instead of 30 t as used by Laws because only adult males are present in the Antarctic and most probably measured over 38 ft in length and more than 30 t in weight before pelagic whaling started. The percentage of the body weight eaten per day is based on Sergeant's (1969) figures of consumption of smaller cetaceans of high protein fishes or squids in captivity. Although this is derived by extrapolation it is probably between 2-3.5% of body weight per day. 3% is taken to allow for the large proportion of ammoniacal squids in the diet which have a calorific value of about half that of muscular squids.

Table 2 shows the genera of cephalopods which live in the Antarctic. Some species that are widely spread in the temperate regions also occur south of the Antarctic Convergence into the low latitudes of the Antarctic. Squid flesh from stomachs of Sperm Whales caught off South Georgia shows that this is true for *Todarodes* sp. (probably *T. filippovae*) *Taningia danae* and *Moroteuthis robsoni*, the beaks of which contribute 2%, 11% and 7% respectively of all beaks collected from whales around South Georgia. These species are large and weigh up to 3.8 kg, 61 kg and 3 kg respectively. In view of the extensive distribution of these squids to the north of the Antarctic Convergence it is quite possible that they migrate south seasonally over a broad front with the southern retreat of the ice edge and therefore represent a very large annual input of biomass into the Antarctic Ocean.

Because of the very large size and initially

TABLE 1

Estimate of the total biomass of squids eaten by some predators in the Antarctic (see text for explanation and references)

	Nos ×10 000	Mean wt t	Total wt 1 000 t	% squid in food	% body wt eaten/day	No of days of yr	Estimated total wt squid eaten per yr ×10⁶
Sperm Whale	8.5	40	3400	95	3	122	11.8
Total Baleen Whales	97.5	–	43125	1?	3.5	122	1.8
Elephant Seal	60	0.5	300	75	6	333	4.5
Crabeater Seal	1500	0.193	2868	2	7	335	1.345
Ross Seal	22	0.173	38	64	7	335	0.571
Weddell Seal	73	0.246	180	11	7	335	0.463
Fur Seal	20	0.050	10	33	7	335	0.077
Leopard Seal	22	0.272	60	8	7	335	0.112
Total Seals							7.07
Wandering Albatross	7	0.009	0.630	80	7	365	0.013
Grey-headed Albatross	38.5	0.0036	1.39	49	7	365	0.017
Black-browed Albatross	1200	0.0035	42	21	7	365	0.225
Total Albatrosses	1263	–	44.45	?30	7	365	0.34
All birds	35000	0.0024	850	24	7	365	13.54
Total estimate							34.21

TABLE 2

The percentage contribution by weight (underlined) of particular genera of cephalopods to the diet of different predators estimated from the number and sizes of beaks. These percentages, together with the estimates of total biomass of cephalopods consumed by each predator (Table 1) were used to calculate the biomass (in 10^6 t and not underlined) for each genus. For explanations of totals (a), (b), and (c) and for references see text.

	Kondakovia		Moroteuthis		Mesonychoteuthis		Ommastrephid		Gonatus		Other squids		Octopods	
Sperm Whale	18	2.1	4	0.47	77	9.09	+				1	0.1		
Baleen Whales	50	0.90	50	0.90										
Elephant Seal	7	0.27	10	0.39					15	0.59	8	0.31	60	2.34
Ross Seal	63	0.36	4	0.02							34	0.19		
Weddell Seal			49	0.23					1		25	0.12	26	0.12
Fur Seal	48	0.40	18	0.15			32	0.27			2	0.02		
Leopard Seal	42	0.05	57	0.07							1			
Wandering Albatross	81	0.01	2						1		16		1	
Grey-Headed Albatross	4						91	0.02			5			
Black-Browed Albatross	1						76	0.17	1		27	0.05	1	
Totals (a)		4.09		2.23		9.09		0.46		0.59		0.79		2.46
(b)		7.14		3.89		15.86		0.80		1.03		1.38		4.29
(c)		9.68		5.28		9.09		1.09		1.40		1.87		5.82

large populations of baleen whales that include Blue, Fin, Sei, Humpback and Minke Whales (Table 1) even if squids contributed as little as 1% to the diet, an appreciable biomass of squids would be involved. This contribution probably is higher for Sei and Minke Whales which are known to take squid in considerable quantities elsewhere in the world but is not known for Blue, Fin and Humpback Whales. We have very little information on the species of cephalopods eaten by baleen whales but *Moroteuthis knipovitchi* has been collected from Fin and Blue whale stomachs (Clarke, 1980 & unpublished). *Mesonychoteuthis hamiltoni* probably lives very deep, as the only capture of a near-adult specimen was at 2 000 m (Clarke, in preparation); there is no evidence at present that it is found at the relatively shallow depths where baleen whales eat krill. Therefore. I have not included *Mesonychoteuthis* in the diet of baleen whales and in the absence of better data have assumed that *Kondakovia* and *Moroteuthis* each contribute 50% of the squids eaten (Table 2).

The food requirements of seals (Table 1) are based upon the stocks and mean weights given by Laws (1977) whose work is based largely on the work of Øritsland (1977). The diet of Elephant Seals at sea is not well known as they fast when onshore but Laws concluded that they probably eat fishes in inshore waters and cephalopods offshore. However, some cephalopod remains were obtained for analysis from Elephant Seals caught at Signy Island (Clarke & MacLeod, 1982); the estimate of 75% cephalopods in the diet must remain a guess at present. All the seals eat some cephalopods and of the six species, the Elephant and Ross Seals very probably consume the greatest percentage of cephalopods. Because the Crabeater Seals have by far the largest stock (over 14 million), even if cephalopods contribute only 2% to the diet, this represents a substantial biomass of over 1 million tonnes. The percentages of the cephalopod species (Table 2) eaten by Elephant Seals, Weddell Seals, Fur Seals, one Leopard Seal and one Ross Seal are based upon analyses in press or preparation (Clarke & MacLeod, 1982a & b). It is unfortunate that information is not available for Crabeater Seals.

Populations of birds and their food have been described by Mougin & Prévost (1980) and Prévost (1981). There are discrepancies in the figures they quote but some can be used for this

discussion. The total number of the 46 species of birds in the Antarctic is estimated at 350×10^6 with a biomass of 0.85×10^6 t. These authors conclude that the birds eat 4.7×10^6 t of food per month, which is 56.4×10^6t per year, or over 66 times their biomass. (This may not be excessive as a recent detailed study shows that 1×10^7 Macaroni Penguins are estimated to eat 28-45 times their body weight during the 116 days of their breeding season at South Georgia (Croxall & Prince, in press)). Cephalopods are estimated to comprise 24% of the food; this represents a biomass of 13.54×10^6 t. Penguins consume 82% of the total cephalopods eaten by birds according to these authors. The cephalopods eaten by albatrosses represent only about 3% of the weight eaten by all birds. However, in the light of recent quantitative data especially relating to Macaroni Penguin diet, Black-browed Albatross populations and King Penguin populations the importance of birds as predators of cephalopods may have been exaggerated by Prévost (J. P. Croxall, personal communication). The species of cephalopods eaten by penguins have not been identified although they have been for three species of albatross (Table 2) (from Clarke, Croxall *et al.*, 1981; Clarke & Prince, 1981).

The weights of the different species of cephalopods (Table 2) in the diets of the predators has been calculated by multiplying their percentage by weight in the diet (see Clarke, 1980 for Sperm Whales; Clarke & MacLeod, 1982a & b for seals and Clarke *et al.*, 1981 for albatrosses) by the weight consumed by the predators (Table 1). The total weight of each cephalopod species eaten by the predators examined is shown in totals (a) of Table 2. If the predators whose cephalopod diets have not been identified ate the same species in much the same proportions the total weight of each cephalopod would be as in total (b). However, we know this not to be true; *Mesonychoteuthis hamiltoni* is eaten only by the Sperm Whale in substantial quantities and probably lives outside the depth range for most seals and birds. Thus its total should not be expanded to take account of the consumption by other predators and totals (c) in which this species is included only for Sperm Whales may give a closer estimate of the true totals consumed. Similarly, however, other genera in Table 2 may prove more or less important than shown in totals (c) when more is known of diets of predators of which the cephalopod proportion has not yet been analysed.

From the data given here combined with that of Laws (1977) the total consumption before whaling of *Kondakovia*, *Moroteuthis*, *Mesonychoteuthis* and octopods probably was about 35 million tonnes. The effect of whaling on the biomass of krill and, indirectly, on the stocks of other predators of krill, has been much discussed (Sayed, 1981). The direct effect on cephalopod populations has been less than for krill but assuming a drop in Antarctic Sperm Whale population to about a half and a very large reduction in the baleen whale stock it would seem that perhaps 7 million additional tonnes of cephalopods are now available as food for predators, other than whales, in the Antarctic.

If we accept that our estimates of cephalopod consumption are to some degree accurate for the predators concerned we might ask what figures should be added to 35 million tonnes for predators not considered, such as other odontocetes and fishes and what 'standing' stock of cephalopods is necessary to allow such a predation.

To sum up, it seems likely that most of the predation on cephalopods is carried out by Sperm Whales, baleen whales, Elephant Seals, Crabeater Seals and penguins (the Adelie is by far the most numerous penguin).

Of these we know too little about the population of Sperm Whales involved, too little about the percentage of cephalopods in the diets of all their predators (except the Sperm Whales) and too little about the cephalopod species eaten by baleen whales, Crabeater Seals and Adelie Penguins. This study clearly indicates that the study of biomass of cephalopods from predators' diets must first include the most numerous and the largest predators of an area. The strategy of such a study in the future should be to (a) define realistic biogeographical limits for the study; (b) find which large and abundant predators eat cephalopods; (c) estimate biomass of these predators and the

biomass they require for food; (d) find the percentage of cephalopods in the diet; and (e) determine the cephalopod species in the diet and their relative proportions by weight. While all these requirements present difficulties, those associated with (d) are often under-emphasised. Where fishes, cephalopods and crustaceans, which are digested at different rates, co-occur, quantitative results obtained by estimating weights from hard parts such as fish otoliths, squid beaks, and crustacean carapaces should be more accurate than merely weighing the flesh remains of each group left in the stomach after partial digestion.

CONSIDERATION OF SPECIES

Although general taxonomic problems and other difficulties associated with identifying beaks make it difficult to identify some cephalopods to species from their beaks (e.g., in Architeuthidae, Cranchiidae) this does not apply to all species. Indeed, where species have very characteristic beaks, are very well known because of large collections, or are from monotypic genera, considerable confidence can be attached to their identification. Table 3 summarises data on the species whose beaks from predators' stomachs have been studied in detail and, together with the flesh remains, can be used with confidence to assess the distribution and relative importance in the diets of predators. Further records of flesh of these species from Sperm Whales caught off Japan (Okutani *et al.*, 1976) and New Zealand (Gaskin & Cawthorn, 1967) have been added.

The species may be grouped into the Antarctic species *Mesonychoteuthis hamiltoni*, *Gonatus antarcticus*, *Moroteuthis knipovitchi*, *Kondakovia longimana* (which possibly may have a close relative in the Arctic seas according to Clarke & MacLeod, 1976) and the species living in temperate and tropical seas. Of the latter *Taningia danae* is very widespread and, almost everywhere, is very important in the diet of Sperm Whales. Similarly widespread species are *Octopoteuthis rugosa*, *Ancistrocheirus lesueuri* and *Lepidoteuthis grimaldii*. Other species such as *Moroteuthis robsoni* and *Histioteuthis miranda* are widespread in the Southern hemisphere but do not appear to extend into the Northern hemisphere. *Moroteuthis robusta* and *Gonatus fabricii* have close relatives in the Southern hemisphere but are themselves limited to the Northern hemisphere. In a few species (* in Table 3) specimens caught in nets indicate that the ranges are greater than shown in Table 3. The maximum sizes and the length of life of the species are indicated in Table 3 by estimates from beak size based upon size relationships and beak growth previously published (Clarke, 1980).

Discussion

It has been shown that useful information can be obtained on the distribution, relative importance and biology of many cephalopod taxa by analysis of the diet of their predators. The biomass of species of cephalopods eaten by well-investigated predators can be estimated, but we are a long way from being able to estimate the total biomass of cephalopods consumed in any particular oceanic region. If this is our aim we must define the biogeographical limits of the region, determine what interchange of fauna there is between regions, find which predators are the principal consumers of cephalopods, determine populations and biomasses of predators, and then study the numbers and weights of the species of cephalopods in the diets of the predators. Although some of these investigations inevitably will be carried out simultaneously or rest on previous work done with different aims, the more these tasks are done out of order the more time will be wasted on predators or cephalopods of minor importance. As we have seen for the Antarctic, potentially large cephalopod consumers like penguins, several odontocetes, Crabeater Seals and fishes require investigation as these species may greatly affect our estimates of cephalopod biomass.

We do not know the total biomass of cephalopods required to sustain the biomass consumed by predators. From the fishing experience of man we might expect this to be many times the biomass consumed (equivalent in fisheries to the catch removed). However, this parallel may be misleading. Sperm Whales prey upon short-lived squids, most of which are probably in their last year of life or even in pro-

TABLE 3

Percentages by weight (to nearest 1%) of squid species which live in area calculated from the number and size of beaks collected from Sperm Whales, other odontocetes (C), Seals (S), Albatrosses (A) and fish (F). Based on data from Clarke (1980) or references cited.

+ indicates that species is known to live in area from presence of flesh but either contributes <0.5% to diet or its % contribution is not known.

W = weight M.L. = Mantle Length Estimated from beaks except M. = measured

	Iceland	Denmark (Clarke & Kristensen)	Spain	Biscay (Clarke & Stevens)	Azores (R. Clarke)	Madeira		Brazil (Clarke *et al.*, 1980)	30°S 33°W W	E	South Africa	South Georgia	Antarctic	W. Australia	Tasman Sea (Clarke & MacLeod, 1982)	New Zealand (Gaskin & Cawthorn)	Chile & Peru	W. Canada	Japan (Okutani *et al.*)	M.L.	Maximum size W Kg	Length of life Yrs
*Todarodes sagittatus**	+	2C							1	11	+, +A, 91A,32S			18							3.8	2
Dosidicus gigas																	32					
*Moroteuthis ingens**																+				40	1.5	
Moroteuthis robsoni									14	5	+,2A		+	3	2							2
Moroteuthis robusta																		62	+			
Moroteuthis knipovitchi											+, +A, 18S		4,48S							40	1.0	
Kondakovia longimana	3?										+,81A, 4A,48S		18, +S							85	33.0	2
Berryteuthis magister																		18	+			
Gonatus fabricii	+	84C		7F																		
Gonatus antarcticus											+,1A		+, +S								0.07	
Pholidoteuthis boschmai					+				19	1	+A			12	4	+				60	5.7	
Ancistrocheirus lesueuri			+		+	+	5	+	11	15	1A			2	1		3		+	37	3.0	2
Octopoteuthis rugosa				4F(?)					6	12				1	1				+	24	0.6	
Taningia danae			83			14	22	+	13	22	+,6A			37	42				+	120	61.0	
Lepidoteuthis grimaldii			2		+	4		+	3	1	1A			4	1	+			+	100	11.0	
*Cycloteuthis akimushkini**								+	1	2				1	+					58	2.1	1
Histioteuthis bonnellii	60		6	2F	+	36																
Histioteuthis b. corpuscula								+	2	6	+A			+	+					7	0.2	
*Histioteuthis dofleini**						2		+										1	+	15(M)	0.5	
Histioteuthis miranda									4	8				4	1					22	0.8	
*Histioteuthis atlantica**									+	+					1	+				7	0.2	
Mesonychoteuthis hamiltoni											+, +A		77							150.0		
*Alloposus mollis**			2			1			+	+	1A									1.0M		
*Vampyroteuthis infernalis**									+	+										10M	2.0	

* *Todarodes sagittatus* Net caught specimens also show this to live throughout the Atlantic and Mediterranean
Moroteuthis ingens The type was from Patagonia, South America
If *Cycloteuthis sirventi* proves to be the same species the range will include the North Atlantic.
Alloposus mollis It is not certain whether Pacific specimens from nets are the same species
Vampyroteuthis infernalis Widespread between 40°N and 40°S
Histioteuthis dofleini also caught in nets in South Pacific (Voss, 1969)
H. atlantica also caught in nets off Chile (Voss, 1969)

cess of dying during spawning when they are consumed (Clarke, 1980). Providing enough squid survive to spawn enough eggs to replace the stock taken by Sperm Whales (assuming they are by far the most important predator), a stable relationship between the whales and the squid populations could be maintained, even if the whale ate a very large proportion of the squids living in their final year. Since physical conditions vary little from year to year in the

deep ocean, the primary influence to change squid populations may well be changes in predation. As the population of a long-lived animal such as a Sperm Whale might be expected to change rather slowly (unless commercial fisheries reduced the stock dramatically) the population of squid might also be relatively stable. However, such an equilibrium, where the population of a short lived species eaten in its final year is controlled by one predator, would be very prone to a dramatic readjustment if commercial exploitation removed the predator. This could well be the case for some deep sea cephalopods such as *Kondakovia longimana, Taningia danae* and *Ancistrocheirus lesueuri* which may have dramatically increased in biomass as a result of removal of the predator by whaling. We do not yet know what other predators might replace the whale in eating the squids but large bottom fishes might well take advantage of large increases in spawning populations of squids on the continental slope where many of these species probably spawn.

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THE PARASITES OF CEPHALOPODS: A REVIEW

CONTENTS

THE PARASITES OF CEPHALOPODS: A REVIEW

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Abstract

The literature and the status of our knowledge of the parasites of cephalopods are reviewed. Published and unpublished records of all hosts examined and parasites encountered are summarized in the text and a table. Of the approximately 650 species of cephalopods known, partial data on parasites are available for only about 150 species. Only two host species, *Octopus vulgaris* and *Sepia officinalis*, have been studied in detail and their total parasite loads documented. In addition to viruses, bacteria and fungi, three phyla of protists and six phyla of metazoans are recognized as symbionts of cephalopods. Several groups, such as the dicyemids, are known to be unique to the cephalopods. Many groups, especially the larval platyhelminths and nematodes, need to be properly associated with their corresponding adult forms. Viruses and fungi are potentially pathogenic to cephalopods and may be important in situations where cephalopods are reared, cultivated or maintained in captivity. Larval anisakid nematodes are a potential human health problem and should be monitored in areas where squids are eaten raw.

Introduction

In view of the important role which cephalopods play in the marine ecosystem and their increased commercial exploitation and consumption, a review of their parasites is both timely and relevant. In this paper I have attempted to bring together and briefly summarize the rather vast literature which deals with all the parasites of cephalopods. The task was not without some obstacles. Many references to parasites are buried in papers which otherwise deal with cephalopods and hence escape notice of parasitologists. Likewise, papers on parasites which list cephalopod hosts may be overlooked by teuthologists. Finally, many Russian and Japanese papers have been hard to track down and obtain and then usually required translation before the contents could be evaluated.

The text of the review is divided into sections by parasite group. In each I summarize the literature and briefly discuss the cephalopod hosts and their parasites. Location on or in the host is specified and information on prevalence and pathology is provided where known. The life cycle of the parasite is outlined and related when possible to the biology and feeding habits of the host. For obvious reasons I devote more space to discussions of parasites which have not been well reviewed. In all cases I provide the currently recognized name of the host cephalopod if it is different from the name used in the original publication. No attempt was made to resolve the many taxonomic problems that exist especially among the larval cestodes and nematodes. This would require more time than could be devoted and in many cases would require critical attention by an expert.

Historically, the first known reference to a cephalopod parasite was in a book by Redi (1684). During the ensuing decades as cephalopods attracted more attention there has been a dramatic increase in the number of phyla and the number of species of parasites recorded from these molluscs. Table 1 lists all the parasites currently known to be associated with cephalopods. In this Table are included all the published and unpublished records I could locate in order to present as complete as possible an overview of the diversity and distribution of parasites and the hosts examined. It can be seen that the total spectrum of organisms living symbiotically with cephalopods is as great as that found on or in most other marine organisms. With the exception of the dicyemid mesozoans and the apostome ciliates, which are unique in their occurrence in cephalopods, the parasite loads most closely parallel the loads in marine fishes.

In the older literature considerable confusion exists. The identifications of the parasites and sometimes even the hosts often are in doubt. In many cases the lack of adequate descriptions and figures makes it impossible to determine

TABLE 1

Summary of all published and unpublished records of cephalopod genera examined for parasites and the parasitic groups encountered.

Host Genera \ Parasite Group	Viruses	Bacteria	Fungi	Sporozoans	Ciliates	Dicyemids	Monogeneans	Digeneans	Cestodes	Acanthocephalans	Nematodes	Polychaetes	Hirudineans	Branchiurans	Copepods	Isopods
NAUTILOIDEA																
Nautilus															●	
COLEOIDEA																
SEPIOIDEA																
Spirula		●			●											
Heteroteuthis		●			○				○							
Euprymna		●														
Rossia		●			○	●		●	●							
Rondeletiola		●				●										
Semirossia		●														
Sepietta		●			○	●										
Sepiola		●			●	●		●	●		●					
Sepiolina		●														
Sepia	●	●	●	●	●	●		●	●		●			●	●	●
Sepiella									●							
TEUTHOIDEA																
Alloteuthis					○		●	●	○		●				○	
Doryteuthis		●									●					
Loligo		●			●		●	●	●		●	●			●	●
Loliolopsis								●			○					
Lolliguncula					○			●			●					
Sepioteuthis						●										
Uroteuthis		●														
Abralia					○				○		○					
Abraliopsis					○			●	○		○					○
Enoploteuthis					○				○		○					
Pterygioteuthis					●			●	○		○					
Pyroteuthis					○											
Thelidioteuthis					○											
Octopoteuthis									○							
Kondakovia									●							
Moroteuthis					○				●		○					
Onychoteuthis					○						●					
Onykia																
Berryteuthis																
Gonatopsis					○											
Gonatus					○				●							
Lepidoteuthis					○				●		●					
Architeuthis									●							
Bathyteuthis																
Histioteuthis					○				○		●					
Ctenopteryx					○											
Dosidicus					○			●	●							
Hyaloteuthis								●								
Illex					●			●	●		●					

Parasite Group / Host Genera	Viruses	Bacteria	Fungi	Sporozoans	Ciliates	Dicyemids	Monogeneans	Digeneans	Cestodes	Acanthocephalans	Nematodes	Polychaetes	Hirudineans	Branchiurans	Copepods	Isopods
Martialia																
Nototodarus									●		●					
Ommastrephes					○			●	●	●	●				●	
Ornithoteuthis								●								
Symplectoteuthis					○			●	○		○					
Todarodes					●			●	●		●				●	
Todaropsis								●	●		●				●	
Thysanoteuthis								●								
Chiroteuthis					○			●	○		○					
Mastigoteuthis					○											
Bathothauma																
Cranchia																
Galiteuthis																
Helicocranchia																
Leachia																
Liocranchia									○							
Megalocranchia																
Phasmatopsis																
Sandalops																
Taonius																
VAMPYROMORPHA																
Vampyroteuthis					○				○		○					
OCTOPODA																
Chunioteuthis									●							
Grimpoteuthis						○										
Opisthoteuthis						○										
unid. cirrate															●	
Bolitaena					●											
Eledonella					○											
Japatella					○			●			○					
Bathypolypus						●										
Bentheledone						●										
Benthoctopus						●									●	
Eledone					○	●		●	●		●				●	
Graneledone						○										
Octopus	●		●	●	●	●		●	●				●		●	
Pareledone						●										
Pteroctopus					●				○							
Robsonella						●		●								
Scaeurgus					○	○			○							
Thaumeledone						○										
Ocythoe																
Argonauta								●								

● Published reports
○ Unpublished records (Hochberg)

whether the parasite was a ciliate, dicyemid, monogenean, digenean, cestode, nematode or even a part of the host. Only a very few groups of parasites have been reviewed critically in the last 50 years, namely: bacteria (Buchner, 1965); chromidinid ciliates (Chatton & Lwoff, 1935; Hochberg, 1971); dicyemid mesozoans (Nouvel, 1947, 1948; McConnaughey, 1949a, 1951); and the digenetic trematodes (Overstreet & Hochberg, 1975). The most recent reference which takes a broader perspective in reviewing both the crustaceans and helminths of cephalopods as a whole is Dollfus (1958). The present paper is the first review which treats all parasites.

Table 1 shows that with few exceptions the total picture for the parasites of cephalopods is inadequately known. To date only 63 genera and about 150 species of cephalopods have been examined for parasites. This represents fewer than half the known genera and fewer than a quarter of the approximately 650 species of cephalopods currently recognized. In only two cases have the total parasite loads been documented, namely, *Sepia officinalis* and *Octopus vulgaris*. Members of several genera of squids have been studied in some detail and these include *Loligo*, *Illex*, *Ommastrephes*, and *Todarodes*.

Almost without exception all large, mature cephalopods are infected with parasites. Viruses, bacteria, fungi, three phyla of protists and six phyla of metazoans have been recorded. Parasites have been recovered from almost all the tissues and organs of cephalopods. In general terms, however, they are most commonly located: (A) on the gills, (B) in the digestive tract, (C) in the 'kidneys' or excretory organs, and (D) in the musculature. The excretory organs are unusual in that they provide a uniquely suitable environment for the establishment and maintenance of parasites and as such have been exploited by a number of phylogenetically distinct groups (Hochberg, 1982a).

Particular attention has been focused on those parasites which may cause problems during culturing activities. At present only viruses and fungi have been implicated as potential pathogens. However, cephalopod mariculture is such a new field that we constantly need to be alert to the presence and effects of parasites in monoculture situations. In particular, we need to investigate infestations of sporozoans, monogeneans, and copepods.

As the search for additional fisheries resources expands, cephalopods are more commonly being marketed for human consumption. In Japan and other countries where cephalopods, especially squids, are eaten raw there is the very real possibility that larval nematodes will be transmitted to humans. Anisakaisis is currently recognized as an important medical problem which warrants further investigation. This is briefly discussed in the nematode section.

The role of cephalopods in the food web is only now beginning to be understood. One way ecological relationships have been elucidated is through examination of parasites. All the evidence at hand indicates that cephalopods play a similar and equal role to fishes in the transmission of parasites in the marine environment. Many species serve as primary hosts for protozoans, dicyemids, helminths, and crustaceans but more commonly cephalopods function as secondary or reservoir hosts for larval stages of digeneans, cestodes, and nematodes and thus play a vital role in the transfer of parasites through the food web to final hosts such as elasmobranchs, fishes and marine mammals.

Although built on the work of many others, this review is still only a beginning. We must continue to survey wild populations and monitor cultivated stocks of cephalopods for the presence of potential pathogens. But, we must also turn our attentions to the critical tasks of unraveling taxonomic problems, completing life cycles, evaluating the effects of parasites on the growth, reproduction and survival of cephalopods and clarifying the details of cephalopod/parasite interactions in the marine environment.

I. VIRUSES AND TUMORS

Viruses and virus-like particles have been observed in several species of benthic cephalopods. Rungger and his coworkers (1971) described an iridovirus associated with

lesions on the arms and mantle of *Octopus vulgaris*. Infected specimens were first discovered in culture tanks at the Stazione Zoologica in Naples, Italy. Naturally infected animals were later collected in the Bay of Naples where a prevalence of 8.4% was recorded for the population sampled. In initial stages, tiny edematous, nodular tumors appear in the muscle tissue of the arms. As the infection progresses the diameters of the lesions increase and nodules spread to other areas of the body. Death occurred 3-5 months after the appearance of visible tumors.

Devauchelle & Vago (1971) reported on a reovirid infecting the cells of the stomach epithelium of *Sepia officinalis*. Virus-like particles have been observed in sections of the renal appendages of several octopod species from New Zealand, Florida and California (Short & Hochberg, unpub.). This virus is found in the nuclei of the renal epithelial cells of the octopus and also in the nuclei of the somatic cells of the dicyemid parasites which attach to the renal appendages (Short & Hochberg, 1969).

A rare benign tumor in the mantle musculature of *Sepia officinalis* was described by Jullien and coworkers (Jullien, 1928b; Jullien & Jullien, 1951; and Jullien, *et al.*, 1951-52). A causitive agent was not identified but inflammations, lesions, and tumors could be induced experimentally by injection of a wide variety of chemical compounds (Jacquemain, *et al.*, 1947; Jullien, 1928a, c, 1940; Jullien *et al.*, 1951-52, 1953).

II. BACTERIA

The presence of symbiotic bacteria or bacteria-like inclusions in association with cephalopods has an extensive literature which has been summarized in the excellent reviews by Harvey (1952) and Buchner (1965). The majority of the papers investigate luminescent bacteria contained within specialized photogenic organs. A discussion of this topic is outside the scope of the present paper. With the exception of the report by Shibata (1953) of luminescent bacteria in the intestine of *Doryteuthis* (= *Loligo*) *bleekeri*, all the remaining publications deal with non-luminous bacteria found on the skin or in the accessory glands.

In most female sepioid and myopsid cephalopods a pair of glandular organs are located at the anterior end of the nidamental glands in close association with the ink sac. As early as 1918 Pierantoni discovered that these accessory glands (= accessory nidamental glands) do not play a true role in reproduction but instead are packed with dense concentrations of rod- and coccoid-shaped bacteria. At the onset of sexual maturation the accessory glands increase in size and become bright orange or red in color (see Richard, *et al.*, 1979). The color is due to carotenoid pigments contained within the bacteria which reside in the accessory glands. The change in color is accompanied by an increase in the number of bacteria present in the glands. Both events imply an intimate symbiotic relationship which is controlled by the host cephalopod.

Pigmented, non-luminescent bacteria recently have been isolated from the accessory glands of *Loligo pealei* (Bloodgood, 1977) and *Sepia officinalis* (Van den Branden, *et al.*, 1980; see also Decleir & Richard, 1972; Van den Branden, *et al.*, 1979). According to Bloodgood (1977) the bacteria form a stable dividing population that presumably benefits from its location within the tubular matrix of the accessory glands. What benefits accrue to the host cephalopods are not known but warrant investigation.

III. FUNGI

In several specimens of *Sepia officinalis* and *Octopus vulgaris* from the Mediterranean Raabe (1934) discovered filamentous fungal thalli penetrating throughout the renal appendages and causing considerable damage to the host tissue. Raabe placed this highly pathogenic fungus in the ascomycete genus '*Aspergillus*'. The systematic treatment of the ascomycetes is subject to considerable controversy, hence, until more material is available Raabe's identification cannot be verified or rejected. It would appear that this parasite is quite rare, since it has never been reported or mentioned again, in spite of the large numbers of

cephalopods subsequently examined in the Mediterranean and elsewhere.

Recently, Polglase (1980) described a pathological condition in *Eledone cirrhosa* which she attributed to the presence of thraustochytrid and labyrinthulid fungi. These highly pathogenic lower fungi are associated with both plant and animal tissues but their roles have rarely been defined. McLean & Porter (1982) suggest that the thraustochytrids, which they consider to be saprobic normally, are merely secondary invaders of the lesions in *Eledone*. In any event, in *Eledone* the two fungi, either singly or in combination, produce ulcerations in the skin, followed by oedema of the body tissues and eventually death.

Originally observed in wild-caught animals, the pathogens rapidly became established in holding tanks in Scotland from which the disease could not be eliminated. The contagious nature of these fungi is such that no octopods could be maintained in a healthy state in contaminated tanks for long periods of time. Polglase's report indicated that captive animals which frequently display skin lesions should be examined carefully to determine if they are infected by contagious fungal pathogens.

IV. SARCOMASTIGOPHORA

Flagellates and amoebae have not been reported in association with cephalopods. However, Brocco (pers. comm.) discovered an unidentified species of dinoflagellate imbedded in the skin of *Octopus dofleini* collected in Washington. Micrographs of the alga in situ show a dissolution of the epidermal layers associated with lesions in the mantle. No further information is available on this parasite.

V. APICOMPLEXA (= SPOROZOA)

The protozoan genus *Aggregata* has a two host life cycle. Sexual stages occur in the digestive tracts of cephalopods and asexual stages infect the digestive tracts of crustaceans. When first reported by Lieberkuhn (1854) *Aggregata* was thought to be a gregarine. It was correctly interpreted as a coccidian by Schneider (1883) though for many years it was placed in the family Aggregatidae (see Pixell-Goodrich, 1914). Fine structure studies by Heller & Scholtyseck (1969a,b, 1970a,b) indicated affinities with *Eimeria* in the family Eimeriidae and this placement has been accepted by most modern protozoologists (see Grell, 1973; Levine *et al.*, 1980).

The best known cephalopod apicomplexan, *Aggregata eberthi*, infects *Sepia officinalis* and *Portunus depurator* in the Mediterranean, English Channel and North Sea (Dobell, 1925). The parasite probably occurs wherever the distributions of *Sepia* and *Portunus* overlap. Two species of *Aggregata* have been reported from *Octopus vulgaris* in the Mediterranean and also in the English Channel. *Aggregata octopiana* was described by Schneider (1875a,b) and *A. spinosa* by Moroff (1906a). The crustacean hosts for these two species are not known.

Moroff (1908) lists an additional nine species which are thought to be synonyms of the species listed above. A number of species have been described from crustaceans in Europe but as yet these forms have not been identified in specific cephalopod hosts. Among these, *Aggregata coelomica* lives in *Pinnotheres* (Leger, 1901); *A. vagans* in *Eupagarus* (Leger & Duboscq, 1903), *A. inachi* in *Inachus* (Smith, 1905) and *A. leandri* in *Leander*, *Solenocera* and *Acanthephyra* (Pixell-Goodrich, 1950; Theodorides, 1965). Several undescribed species are known to occur in *Octopus* species off California and the west coast of Mexico (Hochberg, unpub.), off Florida (McSweeney, pers. comm.) and in the Caribbean off the Virgin Islands (Hochberg & Couch, 1971). The reports by DeHorne (1930a,b) of *Aggregata* in the polychaete, *Nereis*, represent an obvious misidentification.

Aggregata selectively infects the non-cuticularized, nutrient uptake portions of the digestive tract of both cephalopod and crustacean hosts. In cephalopods the parasite is located within epithelial cells of the mucous membrane and in the submucosal connective tissue. As infective stages (merozoites) migrate through the epithelium of the caecum and intestine, the invaded cells die and degenerate. Periodically, necrotic portions of the gut lining are sloughed off and eliminated. In heavy infections the submucosal tissue of the cephalopod

may be almost completely replaced by parasite cells. When *Aggregata* is present in large numbers the mechanical effects of compressing and deforming host tissue may prevent circulation and muscular activity in the gut wall. In *Sepia* the individual infected cells exhibit no apparent response to the presence of the parasite. However, in *Octopus*, the invaded cells may undergo enormous nuclear and cytoplasmic hypertrophy (Brumpt, 1910; Dobell, 1925; Wurmbach, 1935).

The live cycle of *Aggregata eberthi* is one of the classics in parasitology (see Figure 1). Originally outlined by Leger & Duboscq (1906-1908), the cycle later was studied in detail by Dobell (1914, 1925), Naville (1925) and by Bĕlăr (1926). Fine structure studies of a number of the stages in the life cycle have confirmed the observations of earlier workers (see Porchet-Hennere & Richard, 1969-1971; Porchet-Hennere & Vivier, 1970; Vivier, *et al.*, 1970).

The infection is initiated when *Sepia* feed on crabs such as *Portunus*. Ripe, infective stages (merozoites), which reside in the coelom of the crab, are released into the digestive tract of the cuttlefish upon ingestion of the intermediate host. The merozoites actively bore through the epithelial lining of the caecum and intestine of *Sepia* and enter connective tissue cells in the submucosa. Growth occurs as nutrients are taken up from lymph spaces within the connective tissue of the cephalopod host. During gamogony the merozoites are transformed into gamonts of two types. Each macrogamont gives rise to a single macrogamete and as these large cells develop the nucleus approaches the surface of the cell. Development of the microgamete proceeds until large numbers of biflagellated microgametes are produced. Eventually, motile, male gametes are released into the surrounding tissue and enter the macrogametes in the area where the nucleus touches the pellicle.

Following fertilization the zygote undergoes a reduction division which subsequently triggers a burst of mitotic activity. During sporogony the cytoplasm of the sporont is progressively divided up and a large number of sporoblast produced. When finally enveloped by a gelatinous coat the sporoblasts, which now fill the oocyst, are termed spores or sporocysts. In *Aggregata eberthi*, following two additional divisions, each sporocyst contains three sporozoites measuring 8-9 μm.

Mature sporocysts rupture out of the oocyst and are eliminated with the feces. Often entire portions of necrotic gut lining containing intact oocysts are sloughed off and discharged to the exterior. The infection can be experimentally transmitted to crabs by feeding them ripe spores contained in either detrital material contaminated with cuttlefish feces or scraps of cuttlefish intestine. Within a few hours after ingestion, the infective sporozoites are released and move actively about in the lumen of the crab gut. Within 24 hours they will penetrate the epithelial lining of the midgut and migrate into the lymphoid tissues of the submucosa. Here they round up and enlarge into meronts. When growth is completed an asexual phase of reproduction begins. During merogony the nucleus divides many times producing a large number of daughter nuclei which come to lie near the surface of the highly convoluted cytoplasm. After the merozoites are released, there is no further development until the crab is eaten by the cuttlefish and the cycle starts over again.

VI. CILIOPHORA

With the exception of the dicyemids, ciliates are the most frequently encountered parasites of cephalopods. At least five families are parasitic in the renal organs, in the digestive glands and on the gills of cuttlefishes, squids and octopuses. However, only a few published studies deal with these unusual forms and many new findings await analysis.

The genus *Chromidina* is restricted to a small group of vermiform ciliates which attach to the appendages within the renal or renal-pancreatic coela of cephalopods. Only three species have been described, though a total of 23 species of cephalopods in 20 genera currently are known to harbor chromidinids (Hochberg, 1982a). In the Mediterranean and English Channel, *C. coronata* occurs in *Octopus vulgaris*, *Sepiola rondeleti*, *Illex coindetti*, *Eledone cirrhosa* and *Scaeurgus unicirrhus*. A second species, *C. elegans*, lives in *Sepia elegans*, *S. orbignyana* and *Illex coindetti*. For details see Chatton &

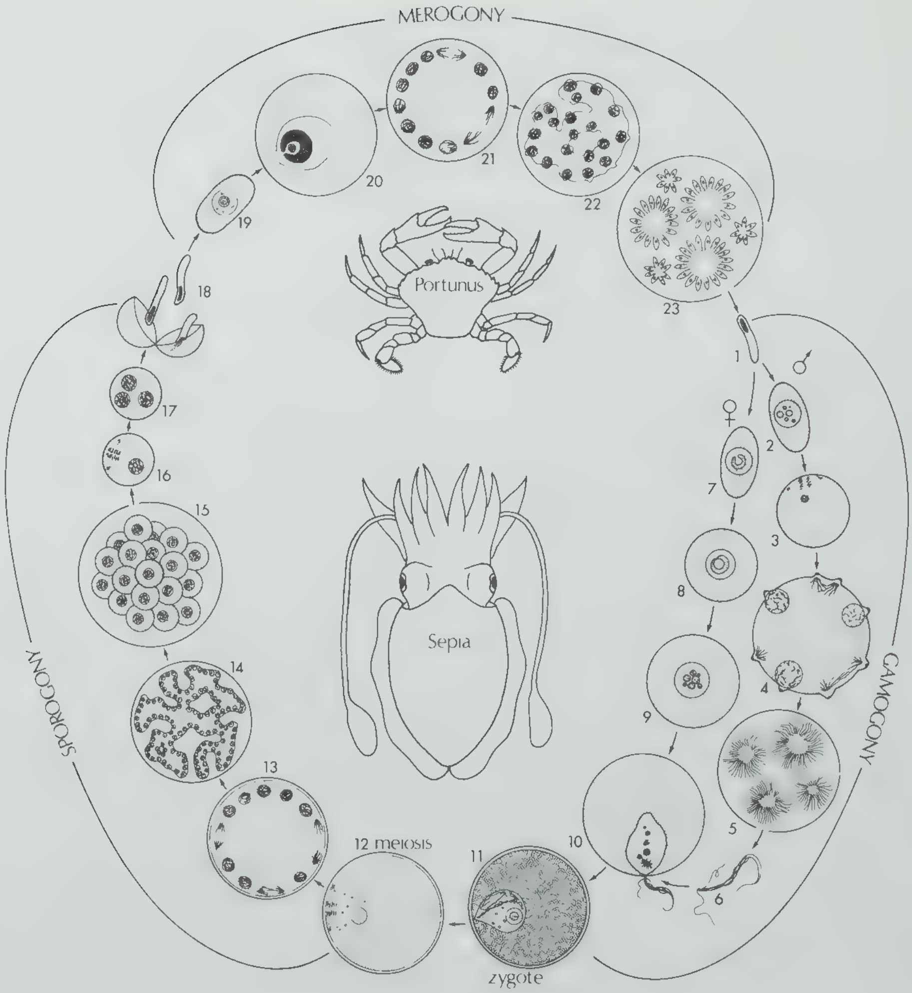

Figure 1. Life cycle of the eimeriid apicomplexan, *Aggregata*. (after Dobell, 1925 and Grell, 1973).
1. merozoite
2-5. microgamont development
6. microgamete
7-9. macrogamont development
10. macrogamete at time of fertilization
11. zygote
12-14. sporont development
15. oocyst with developing sporocysts
16-17. sporocyst development
18. sporocyst (spore) with 3 sporozoites
19-23. meront development

Lwoff (1928, 1931, 1935); Collin (1941b, 1915); Dobell (1909); Foettinger (1888a,b); Gonder (1905); Hochberg (1971); and Nouvel (1935a,b,c, 1937, 1945). A third species, reported from *Pterygioteuthis giardi* in the Gulf of California, Mexico, is treated by Hochberg (1971).

Ciliates, attributed to *Chromidina elegans*, have been reported from *Todarodes sagittatus* and *Octopus salutii* in the Mediterranean (Nouvel, 1945; Hochberg, 1971); from *Loligo* sp. off Russia (Wermel, 1928); and from *Spirula spirula* in the Atlantic Ocean (Clarke, 1970; Jepps, 1915). This material has not been critically examined and compared to the type species and hence the true designations are not known. In the North Pacific Ocean a wide variety of schooling epi- and mesopelagic cephalopods are infected. Of these oceanic

cephalopods, *Chromidina* infects species of the following genera: *Heteroteuthis*, *Abralia*, *Abraliopsis*, *Pterygioteuthis*, *Ctenopteryx*, *Mastigoteuthis*, *Histioteuthis*, *Dosidicus*, *Symplectoteuthis* and *Japatella*. Several undescribed species are involved (Hochberg, in prep.).

Characteristically only truly pelagic squids and octopods are infected. Infection of benthic or epibenthic hosts occasionally has been reported but in all of these cases the ciliates were found only in octopods which have planktonic larvae (i.e., *Octopus salutii*, *O. vulgaris*, *Scaeurgus unicirrhus*, and *Eledone cirrhosa*) or in sepioids whose young feed in surface waters (i.e., *Sepia elegans*, *S. orbigiana* and *Sepiola rondeleti*).

As elucidated by Hochberg (1971, see also 1982a) *Chromidina* has a two-host life cycle (see Figure 2). Like the better known foettingerids, it undergoes a complex polymorphic cycle involving an ordered sequence of distinct phases. Young squids pick up ciliates when they associate with or feed on swarms of pelagic crustaceans, such as euphausiids. At present the method of entry into the host is not known. Within the cephalopod, the stages of the cycle are considerably modified and condensed, compared with the small, ovoid, and less specialized foettingerids (see Bradbury, 1966; Chatton & Lwoff, 1935). In *Chromidina*, the vegetative and divisional phases are combined into long, thin tropho-tomonts. These vermiform individuals attach to the renal appendages by means of a thigmotactic anterior end. The remainder of the body, which is actively involved with nutrient uptake and division, hangs free in the fluid-filled coelomic space. Reproduction takes place by unequal, transverse fission or budding at the posterior end of the body.

Two distinct budding patterns are observed, monotomy and palintomy. In young hosts, the ciliates all produce large, single buds, termed apotomites, which resemble the parents. When detached they are transformed directly into second generation tropho-tomonts. By means of this initial budding process the number of ciliates is continually increased within the renal sacs until eventually the renal habitat is saturated with ciliates. The second divisional phase, palintomy, is probably triggered by chemical factors related to the density of parasites or maturation of the host. During palintomy, a multiple fission process takes place which produces long chains of 8, 12, or 24 small buds. Tiny, ovoid dispersal stages, termed tomites, eventually are formed which bear little resemblance to the parent tropho-tomonts. The tomites conjugate immediately after detachment from the parent, and then exit through the renal pores to the exterior with the passage of urine.

Once in the sea, the ciliates swim about until they contact a euphausiid or other appropriate crustacean host. The tomites then encyst on the mouth parts and setaceous appendages of the new host. During this phoretic stage, the ciliates undergo several growth phases. Euphausiids are known to molt every few days. As in other apostome cycles, it is presumed that the ciliates encyst with each molt, feed, grow, and then recyst on another host crustacean (see Bradbury & Trager, 1967; Trager, 1957). Eventually they attain a size which is capable of infecting a cephalopod, and the cycle begins again.

The maximum length of vermiform stages in the cephalopod renal organs ranges from 400 to 2 000 μm depending on the species. Two basic body shapes occur. *Chromidina coronata* has an inflated anterior end and a conspicuous crown of elongate cilia whereas in *C. elegans*, the anterior end is not swollen and the ciliary crown is lacking. In other ways the species are almost identical. The infraciliature of the tropho-tomonts consists of a tight dextral helix, continuous without breaks from the anterior to the posterior pole. Typically 12-14 kineties are present. The macronucleus is an open network of chromatin found throughout the entire body. A tiny spindle-shaped macronucleus is located in the posterior end of the body in the region of the future fission plane. The appearance of trichocysts in the posterior region of the body signals the onset of division. Unlike the foettingeriids, full grown vegetative stages do not encyst prior to division. Mouth, rosette and contractile vacuole, typically found in the foettingeriids, are absent in the stages within the cephalopod host. During palintomy the

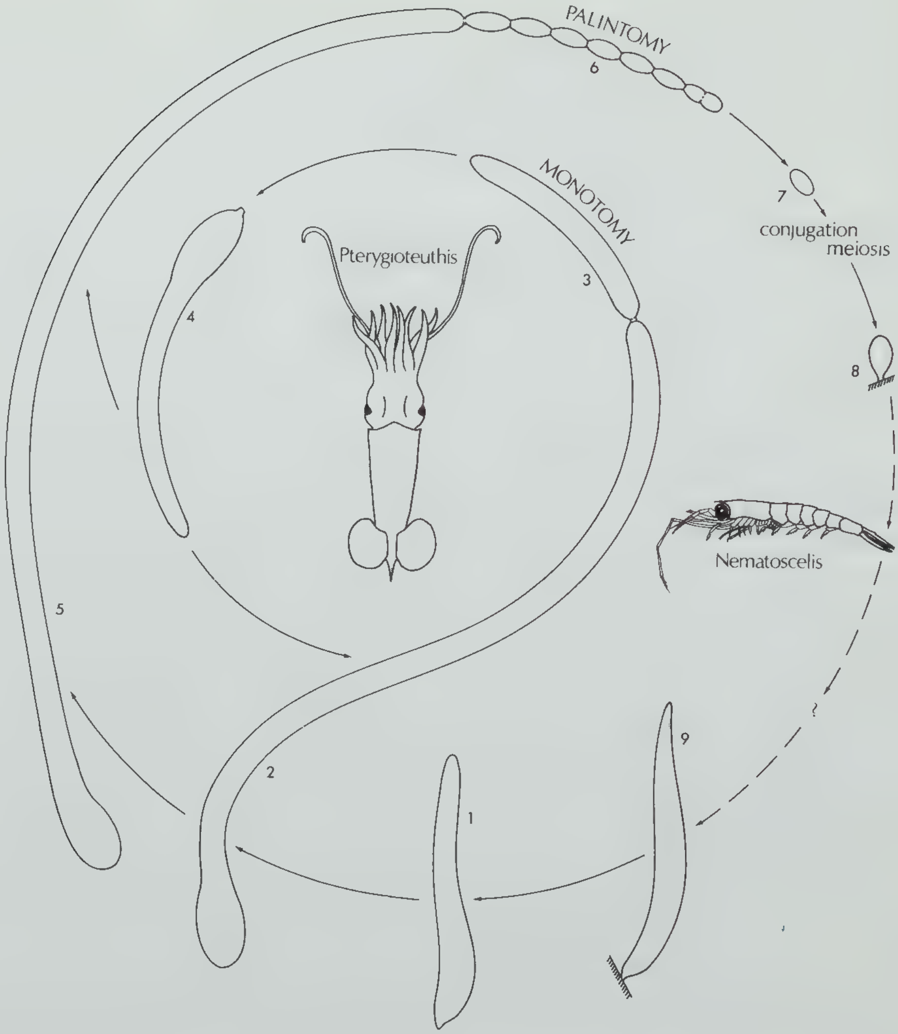

Figure 2. Life cycle of the apostome ciliate, *Chromidina*.
1. protropho-tomont
2. 1° tropho-tomont
3. production of apotomite via single fission
4. apotomite
5. 2° tropho-tomont
6. production of tomites via multiple fission
7. tomite detached from parent
8. 1° phoront
9. 2° phoront

kineties are shortened and straightened with each successive division. The oral field and contractile vacuole develop after detachment from the parent. The appearance of the nuclei also alters markedly during palintomy, as shown by Chatton & Lwoff (1935) and Hochberg (1971). Fully developed tomites range in size from 15 to 30 μm. They are pyriform in shape with a convex dorsal surface and a flat or slightly concave ventral surface. Hovasse (pers. comm.) observed conjugation immediately following release of the tomites.

Occasionally hypertrophonts, measuring up to 5 000 μm, are found. Described by Collin (1914b, 1915) these degenerative individuals appear to have penetrated the epithelium of the reno-pancreatic appendages and entered the blood spaces within. Here they increase rapidly

in size, probably because of high osmotic pressures. The nuclei undergo caryolysis and the cilia are lost.

Small, ovoid infusorians infecting the midgut and digestive glands of cephalopods are placed in the related genus, *Opalinopsis*. Two species have been described from the Mediterranean and the English Channel. *Opalinopsis sepiolae* is reported from *Sepia rondeleti*, *Sepia elegans* and *S. officinalis* (see Collin, 1941b, 1915; Dobell, 1909; Foettinger, 1881a,b; Gonder, 1905). I have observed what is probably the same species in *Sepiola atlantica*, *Sepietta oweniana*, and *Rossia macrosoma*. *Opalinopsis octopi* has been obtained from *Pteroctopus tetracirrhus* and *Octopus macropus* at Naples and Banyuls (Foettinger, 1881a,b; Hochberg, 1971). Collin (1914a) described a third species of *Opalinopsis* from the heteropod mollusc, *Carinaria mediterranea*, collected at Villefranche. This later species has not been studied since first described and should be reexamined. Collin (1914a) promised a review of the genus *Opalinopsis* but it was never forthcoming. Recently, I have found several undescribed species of *Opalinopsis* in *Heteroteuthis*, *Histioteuthis* and *Japatella* off Hawaii and Baja California, Mexico (Hochberg, 1982b).

The life cycle of the opalinopsids is incompletely known. In the cephalopod host, tropho-tomonts of *Opalinopsis* move freely through the digestive gland and the digestive gland appendages ('liver', 'pancreas', and 'hepatopancreas' of previous authors). Division is equatorial and monotomic. Long chains of buds are not produced nor is sexuality known. Stages outside the cephalopod are not known.

The taxonomic position of *Opalinopsis* and *Chromidina* has been subject to considerable debate. In the past both genera were most often treated together. An affinity between these two genera of highly specialized cephalopod parasites and the apostome ciliates was first proposed by Chatton & Lwoff (1926). Their ideas regarding this relationship were later expanded (1928, 1930), and in 1931 they reported stages in the life cycle of *Chromidina* that were very similar to the foettingeriids. In reviewing the systematic literature (Hochberg, 1971) I pointed out the distinctness of the two genera and placed each in its own family. I also reaffirmed placement of the chromidinids in the Order Apostomatida. The opalinopsids, on the other hand, are regarded as perhaps outside the defined limits of the apostomes (Chatton & Lwoff, 1935; Hochberg, 1971, 1982b).

VII. DICYEMIDA

The dicyemid mesozoans are a small and puzzling group without definite affinities in the animal kingdom. They exhibit an impressive array of truly unique characters which hold a special curiosity for zoologists. They were first described by Krohn (1839). Later, Erdl (1843) observed that they produced two kinds of embryos but it was not until 1849 that von Kölliker gave them the generic name, *Dicyema*, to denote this alteration of stages. Beneden (1876) believed that these simple, cell constant organisms linked the protozoans and the metazoans and hence he proposed the name, Mesozoa. The dicyemids, along with the orthonectids, have long been considered a Class within the Phylum Mesozoa (see reviews by Czihak, 1958; Dodson, 1956; Grassé, 1961; Hyman, 1940, 1959; McConnaughey, 1963, 1968; Mendes, 1940; and Stunkard, 1954). The orthonectids parasitize a number of marine invertebrate phyla: Platyhelminthes (turbellarians); nemerteans; annelids (polychaetes); molluscs (gastropods, bivalves, but *not* cephalopods); echinoderms (ophiuroids); and chordates (ascidians). In light of dissimilar internal features and the lack of homologies in stages of life cycles, it is best to treat these two assemblages as separate phyla and to use the term 'Mesozoa' to refer to their grade of organization only.

The dicyemids are the most common and characteristic parasites of the excretory organs of cephalopod molluscs. These minute, vermiform organisms attach principally to the renal appendages while the remainder of their worm-like bodies float in the fluid-filled renal coelom. In decapods they are found additionally in the reno-pancreatic coelom attached to the digestive duct appendages and very rarely are located in the pericardium attached to the branchial heart appendages. They live and re-

produce in these organs doing no apparent harm to the host.

A total of 59 species of cephalopods, representing 18 genera, are currently known to host dicyemids (see Table 1). They occur in sepioids, especially cuttlefishes and sepiolids, and also in octopods in both cirrate and incirrate groups. Among the teuthoids, only *Sepioteuthis*, an epibenthic loliginid, has been reported to be infected. Each cephalopod host species harbors either a single species of dicyemid or a complex of species that are most often distinct at the generic level. As examples: *Octopus rubescens* hosts *Dicyema balamuthi*, *Dicyemennea adscita* and *Conocyema adminicula* (Hochberg, 1971; McConnaughey, 1949a); *O. tehuelchus* harbors *Dicyema australis*, *Dicyema platycephalum* and *Conocyema marplatensis* (Penchazadeh, 1968, 1969, Penchazadeh & Christiansen, 1970); *Benthoctopus magellanicus* is infected with *Dicyema benthoctopi* and *Dicyemennea littlei* (Hochberg & Short, 1970); and *Sepia officinalis* may concurrently host *Dicyemennea gracile*, *Pseudodicyema truncatum* and *Microcyema vespa* (Nouvel, 1947).

Dicyemids parasitize only benthic or epibenthic cephalopods although the distribution is by no means universal. In temperate and polar waters adult, benthic cephalopods generally are 100% infected. In subtropical waters the prevalence of infection varies but is always less than 100%. In the tropics and off oceanic Islands no cephalopods have been reported to be infected. The reasons behind these distribution patterns are not known.

Initial infections normally occur in very young animals, either immediately following hatching, as in cephalopods with demersal juveniles, or following settlement to the bottom, as in those host species with planktonic larval stages. In all the cephalopods I have examined I have never encountered dicyemids in neritic or oceanic species. McConnaughey (1959) reported a species of *Dicyemennea* in *Loligo opalescens* and Aldrich (1964) reported a single dicyemid in a single specimen of *Illex illecebrosus*. Both *Loligo* and *Illex* are neritic genera and hence these reports are probably in error. Thousands of specimens of *Illex* and *Loligo* have been examined by many investigators and none have been infected with dicyemids.

Nouvel (1947) and McConnaughey (1949a) reviewed the dicyemids and hosts known until then. Since that time a number of species have been described from a variety of geographical localities: East coast of Russia (Bogolepova, 1957; Bogolepova-Dobrokhotova, 1960, 1962); France (Nouvel, 1961); Florida and the Gulf of Mexico (McConnaughey & Kritzler, 1952; Couch & Short, 1964; Short, 1961, 1962, 1964); West coast of North America (McConnaughey, 1949b, 1957, 1959, 1960; Hoffman, 1965); Argentina (Penchaszadeh, 1968, 1969; Penchaszadeh & Christiansen, 1970); New Zealand and the Antarctic (Hochberg & Short, 1970; Short, 1971; Short & Hochberg, 1969, 1970; Short & Powell, 1969).

To date 65 species of dicyemids have been described. If we add to this the undescribed species in several collections and the number of potential host species still to be examined, it is possible to project a total of about 200 species in the phylum. Seven genera are currently recognized and placed in two families—DICYEMIDAE: *Dicyema* (32 species), *Dicyemennea* (25), *Dicyemodeca* (2), *Pleodicyema* (1), and *Pseudicyema* (1); CONOCYEMIDAE: *Conocyema* (4 species), and *Microcyema* (1).

Genera are determined by the number and orientation of cells in each tier of the calotte, the presence or absence of abortive axial cells and the presence or absence of syncytial stages. Species are characterized by the size of the adult stages, the number of cells comprising the body, the shape of the calotte, the anterior extension of the axial cell, the presence or absence of verruciform cells and the structure of the infusiform larvae. Recent description of new species from a number of new host genera has greatly expanded our ideas about the morphological characteristics of the phylum as well as helped to define the limits of geographic distribution and host specificity.

Close examination of the dicyemids reveals a simple structure. In the adult vermiform stages, called nematogens and rhombogens, a single internal, axial cell runs almost the entire length of

the body (Figure 3). The total length of the vermiform stages ranges from 500 to 10 000 μm, depending on the species. Reproductive products are relegated to the interior of the axial cell of the parent, which functions as a nurse or follicular cell providing both protection and nourishment for the germ cells and developing embryos. The axial cell is surrounded by a jacket of 20 to 40 large ciliated cells, called somatic or peripheral cells, The number of cells in the jacket is species specific. The head or anterior end is modified into a calotte, by which the parasite attaches to the host renal tissue.The calotte is covered by short stiff thigmotactic cilia which interdigitate with the brush border of the renal epithelial cells. The actual shape of the calotte varies a great deal depending on the species. There is no trace of a differentiated digestive, circulatory, nervous, respiratory, glandular or excretory system. No muscles, sensory receptors, or skeletal elements are present. In fact, nothing comparable to organs, tissues or glands is observed.

The infusiform, or dispersal stage, is morphologically the most complex stage in the life cycle, and yet, it is remarkably similar from species to species. It has been described in detail by Nouvel (1933a, 1948, 1961) and Short & Damian (1966). Mature larvae are ovoid. All species are ciliated posteriorly and most have two large refringent bodies anteriorly. They range in length from 25 to 50 μm and have a total of either 37 or 39 cells. Internally there is an urn cavity filled with four large cells each containing a smaller germinal cell. A relatively large nucleus and the intracellular location of these small cells indicates that they are probably germinal cells which give rise to the next generation. Recent fine structure studies by Bresciani & Fenchel (1965, 1967); Ridley (1968, 1969); and Matsubara & Dudley (1967a,b) have helped to clarify and resolve many observations on both the vermiform and infusiform stages in the life cycle.

The life cycle (Figure 3) has been a subject of controversy and, in spite of extensive study, it is still incompletely known (see papers by Gersch, 1938a,b, 1941a,b; Hartmann, 1904, 1906, 1925; Hochberg, 1982a; Koeppen, 1892; Lameere, 1905-1923; McConnaughey, 1951; Nouvel, 1947, 1948; Stunkard, 1937, 1954; Wheeler, 1899; Whitman, 1883). In its simplest expression it consists of an alteration of essentially isomorphic, parent generations. The embryos of all known stages develop within the axial cell of the parent until they are released through rupture of the parent's body wall. Cleavage is determinant, and a definite cell number is attained early in development. Subsequent growth is by cell enlargement.

The mode of entry into the host and the initiation of the infection is not known. Lapan & Morowitz (1972) proposed that germinal cells from the urn of the infusiform could directly infect the circulatory system of the host and from there penetrate into the kidneys. However, they did not present evidence or experimental data to support their contention. The earliest known stage observed in juvenile cephalopods is termed a stem nematogen. This stage differs from the typical adult vermiform stages principally in having two or three axial cells instead of the usual one. Subsequently, however, these stem nematogens produce vermiform embryos which have only one axial cell (see Figure 3).

The stage of the dicyemid cycle appears to depend on the maturity of the host. Immature hosts harbor populations of nematogens, all of which contain elongate vermiform embryos in their axial cells. The embryos develop asexually from gametes (axoblasts) and resemble the parent nematogens by the time they are released. Constant proliferation of daughter nematogens eventually results in an enormous population of dicyemids which fills the renal organs of the cephalopod host.

In older hosts the adult vermiform stage is called a rhombogen. In the axial cell of this parent stage the vermiform embryos are replaced by gamete-producing infusorigens and infusoriform larvae. Long a subject of controversy the hermaphroditic infusorigen has been described as either an individual or a gonad. The infusorigen consists of a nearly spherical axial cell which contains all the developmental stages leading to mature spermatozoa, and a jacket composed of oogonia and oocytes. Amoeboid spermatozoa emerge from the axial cell and penetrate peripherally

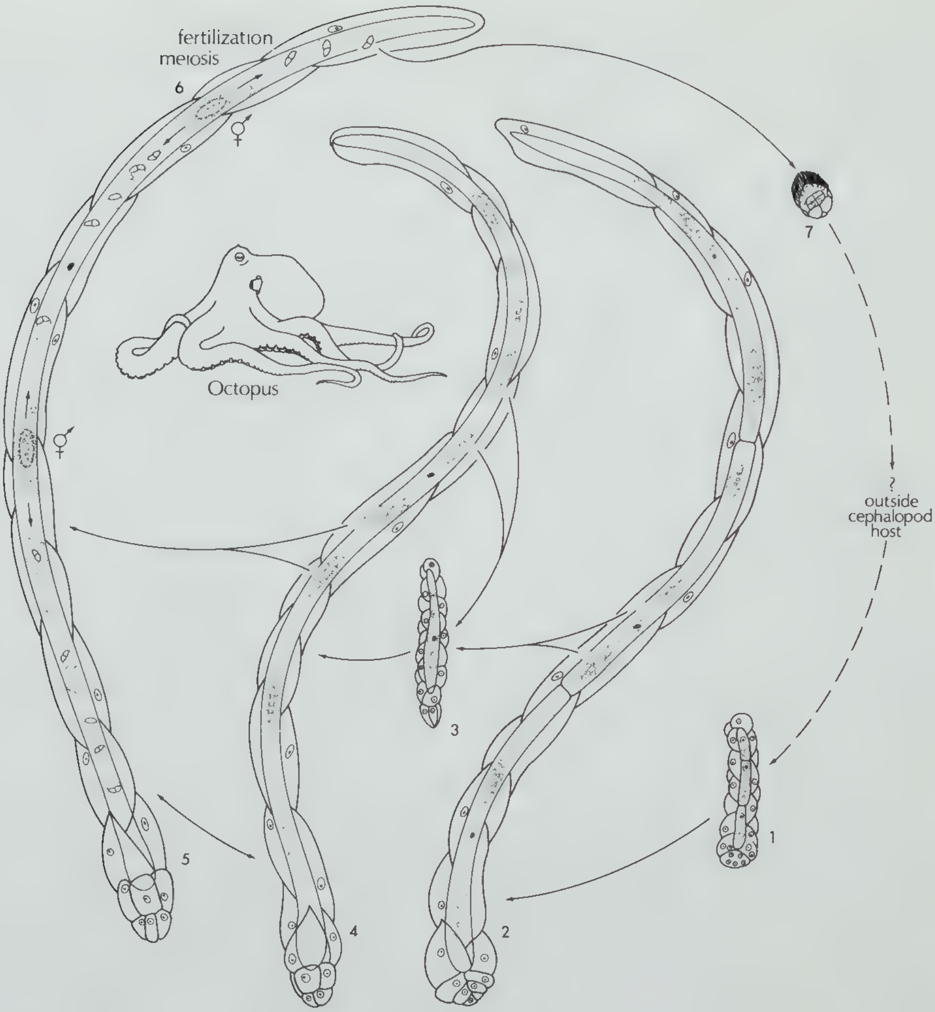

Figure 3. Life cycle of the dicyemid mesozoan, *Dicyemennea.*
1. larval stem nematogen
2. stem nematogen
3. vermiform embryo
4. nematogen
5. rhombogen
6. infusorigen
7. infusoriform released from parent

located oocytes (Austin, 1964; Short & Damian, 1967). The resulting zygotes develop into ovoid embryos which, when full grown, are termed infusoriform larvae. After breaking out of the parent body, the infusoriforms escape from the renal environment with the passage of the urine. The fate of this dispersal stage and the phase(s) of the cycle which occur(s) outside the cephalopod host are still a mystery. Several authors have suggested that the infusoriform larvae or their released germinal cells must infect a secondary benthic host since they are not attracted to young cephalopods (see Nouvel, 1947; McConnaughey, 1951; Stunkard, 1954). On the other hand, Lapan & Morowitz (1975) recovered dicyemids in the renal organs of *Sepia* reared from eggs in isolated aquaria and exposed only to infusoriform larvae. This indicates that an intermediate host may not be necessary.

Twice during the course of an infection the parasites undergo a change of phase. The initial infective phase is brief, and when the stem nematogens are spent they disappear and are replaced by nematogens. As the cycle progresses all nematogens are eventually transformed into rhombogens during which stage gametic reproduction takes place. In octopods, the transition from nematogens to rhombogens is prolonged and a mixture of stages is often found (Hochberg, 1971), whereas, in cuttlefishes a rapid metamorphosis is completed at the time of sexual maturation of the host (Nouvel, 1933b). Because the shift in phase is particularly evident in adult cephalopods, most authors have suggested that the hormonal flux associated with host maturation acts as a trigger. However, at the time of transition the renal organs are maximally crowded with parasites. Lapan & Morowitz (1975) demonstrated that population pressure or crowding may be the key factor which initiates the shift from the nematogen to rhombogen phase.

Both dicyemid mesozoans and chromidinid ciliates live in the excretory organs of cephalopods. Concurrent infections rarely occur since the hosts of these two parasites are normally spatially isolated. *Chromidina* typically infects oceanic cephalopods which never contact the bottom, whereas, the dicyemids are known from exclusively benthic or epibenthic hosts. The exploitation of the 'kidneys' of cephalopods by these two unusual vermiform parasites, therefore, is facilitated and maintained by the habits of the hosts and the spatial separation of the infective stages. In the absence of competition, adaptation to the selective pressures within the excretory environment has favored convergence of both form and reproductive strategy. In addition to the sizes and shapes of all stages being nearly similar, both parasites exhibit a diphasic life cycle which is remarkably well adapted to the requirements of their endoparasitic existence (Hochberg, 1982a).

VIII. PLATYHELMINTHES

A. Monogenea

Several monogeneans have been described from cephalopods. These forms are reviewed or figured by Bychowsky (1961), Dollfus (1958), Palombi (1949) and Sproston (1946).

Delle Chiaje (1822) recorded *Polystoma loliginum* from *Loligo vulgaris* in the vicinity of Naples, Italy. In 1841, he related that Krohn had discovered a similar monogenean in the vena cava of *Sepia officinalis*. Later, Diesing (1850) described *Solenocotyle chiajei*, which is now considered to be a synonym of *P. loliginum*. The existence of this species is the center of considerable controversy, as described by Dollfus (1913). This unusual endoparasitic worm is reported to infect the large blood vessels of at least two cephalopod hosts as mentioned above.

Two species of the genus *Isancistrum* have been found on adult *Alloteuthis subulata* (in older literature referred to as *Loligo media*) captured in the English Channel off France and England. Beauchamp (1912) originally described *I. loliginis*, which is now known to occur in small numbers (hundreds) in the mantle cavity and attached to the ends of the gill lamellae in the squid host (Sprehn, 1933; Llewellyn, 1974; see also Anon., 1976). A second, undescribed species lives in very large numbers (thousands) on the arms and tentacles of *Alloteuthis* (Llewellyn, 1974, 1979). These tiny, transparent parasites are viviparous gyrodactylids, which lack a free swimming larval stage. Llewellyn demonstrated that they invade new hosts by direct transfer during copulation. His studies also indicated the presence of overlapping generations of squid, which is an essential condition for survival and perpetuation of these two monogeneans.

Immature specimens of a third genus of monogenean were collected at Woods Hole, Massachusetts on an unidentified squid (probably either *Loligo* or *Illex*). This worm was originally assigned to the genus *Erpocotyle* by Price (1942). Though transferred to the genus *Squalonchocotyle* by Sproston (1946), Yamaguti (1963) later reassigned the original genus name. Until more material is available the exact generic placement and the specific name remain in doubt.

As more cephalopods, especially loliginids, are critically examined for parasites monogeneans may be shown to be common.

B. Digenea

Until recently cephalopods attracted little attention as potential hosts for digenetic trematodes. However, reviews by Overstreet & Hochberg (1975) and Gayevskaya (1977b) point out that almost 20 species of digeneans have been recovered from a total of nearly 30 species of cephalopod hosts (see Table 1). Cephalopods are parasitized by either larval stages (metacercaria) or adults and, hence, act as second intermediate, paratenic or final hosts but never first intermediate hosts.

The most characteristic and quantitatively the most important group of digeneans which infect squids are the larval didymozoids. Several distinct species are recognized that differ in body dimensions and the presence or absence of a thick walled stomach. In the majority of cases it has not been possible to associate these metacercarial stages with specific identified adult worms, hence, most are collectively lumped under the names '*Monilicaecum*' and '*Torticaecum*'. For a list of hosts and parasites see: Belyaeva (1979); Dollfus (1971); Fields & Gauley (1972); Gayevskaya (1976, 1977a,b); Gayevskaya & Nigmatulin (1975, 1976b, 1977, 1978); Hochberg (1969a); Overstreet & Hochberg (1975); Naydenova & Zuev (1978); Reimer (1974); and Yamaguti (1942).

Didymozoid metacercaria are localized in cysts adjacent to major blood vessels in the external wall of the stomach and caecum of most hosts. In certain tropical regions the prevalence of infection in oceanic squids may reach 100%, especially in the enoploteuthids and ommastrephids. Often hundreds or even thousands of worms may occur in a given host individual. Prevalence and parasitic load increase with an increase in the size of the host and with variations in diet. Maximum infections occur in squids which are intensively feeding on planktonic crustaceans and on small planktivorous fishes (Gayevskaya & Nigmatulin, 1977; Hochberg, 1969a). Gayevskaya (1976) proposed that infection may be initiated by free floating cystophorous cercariae which enter the mantle cavity and are 'fired' into the tissue of the host.

The life cycle of the didymozoids is thought to involve four hosts, but this has not been confirmed experimentally. The first intermediate stage probably occurs in pelagic molluscs, such as heteropods and thecosomes. The second intermediate or metacercarial stage occurs in crustaceans, such as copepods (Madhavi, 1968; Reimer, *et al.*, 1971). A third intermediate stage may occur in planktivorous fishes and squids. Hochberg (1969a) observed excysting metacercariae in squid stomachs filled with crustacean parts. Adult didymozoids occur in final hosts such as the large predatory tunas and billfishes.

Two genera of metacercariae are known from octopods, *Elytrophallus* from *Japatella heathi* and *Stephanostomum* from *Octopus briareus*. The latter is noteworthy because it is one of only a few digeneans known to infect its cephalopod host by active cercarial invasion rather than through ingestion of the metacercaria.

A number of immature, progenetic, and even a few sexually mature, adult digeneans have been reported. Two derogenids, *Derogenes varicus* and *Gonocerecella sepiocola* occur in *Sepia officinalis* (Overstreet & Hochberg, 1975; Reimer, 1974, 1975). The worms found in *Sepia* by Gros (1847) and Vaullegeard (1896) were probably *D. varicus*. *Gonocercella sepiocola* is not well known but *D. varicus* is considered by some to be the most widely distributed of all animals. It occurs world wide and has been reported from a great diversity of fishes and invertebrate hosts. Køie (1979) reviewed the life cycle and redescribed several of its stages. Redia and cystophorous cercariae develop within the first intermediate host, which are gastropods of the genus *Natica*. When released the free swimming cercariae enter copepods and develop into metacercaria. When the copepods are ingested by larger crustaceans and chaetognaths the metacercaria may mature into adult worms, though usually *Sepia* and a variety of fishes are regarded as normal final hosts to the adult stage. Immature and even egg bearing progenetic worms may be transferred from one fish to another fish or to a cuttlefish.

In New Zealand, the allocreadiid, *Plagioporus maorum* commonly infects *Octopus maorum* and occasionally occurs in *Robsonella*

australis (Allison, 1966; Short & Powell, 1968). Typically 40% or more of these octopods are infected. The renal sacs and adjacent areas often contain 30 or more worms. The presence of sexually mature, adult worms indicate that these octopods can be regarded as final hosts and not merely intermediate hosts.

Most reports of trematodes in cephalopods are discoveries of single hemiurids, accacoelids and hirudinellids. Typically, the prevalence of infection is low. As a result, cephalopods are not thought to play an important role in the life cycle of most digeneans. In most cases, cephalopods probably function simply as paratenic hosts which acquire infections when they eat the same intermediate hosts normally consumed in large numbers by teleosts which serve as the final hosts. As examples, in the Atlantic, Gayevskaya (1977a) found *Hirundinella ventricosa* in fewer than 1% of the *Ommastrephes pteropus* examined, and in Mississippi, Overstreet & Hochberg (1975) reported *Lecithochirium microstomum* in only 10% of the *Lolliguncula brevis* examined. Thus, these 'accidental' occurrences are due to ecological similarities between cephalopods and fishes in the pelagic environment.

C. Cestoda

Adult cestodes have never been reported from cephalopods. However, a diversity of larval and post-larval stages repeatedly have been described from decapods and octopods. This diversity indicates that cephalopods are important as second intermediate or paratenic hosts for cestodes which mature in elasmobranchs and fishes, and are transferred from host to host through the food chain.

Two orders of cestodes are represented in cephalopods, namely the Tetraphyllidea and the Trypanorhynchidea. Adults in both groups parasitize the digestive tracts of sharks, skates, and rays. Life cycles have not been completed for either of these two orders although several possible patterns have been postulated. At least two and sometimes three intermediate hosts and as many morphological forms of the parasite are involved (Euzet, 1979; Mudry & Dailey, 1971; Overstreet, 1983). In general terms, eggs, each containing a ciliated larval stage, are discharged from the vertebrate definitive host with the feces. Once in the sea the eggs are ingested by crustaceans, especially copepods and euphausiids. In the first intermediate host the oncospheres (=hexacanths) penetrate the intestine and undergo metamorphosis in the hemocoel to form procercoids. When the copepods are ingested by large teleost fishes, like sciaenids, the procercoids develop into solid-bodied post-larvae or plerocercoids. Recent evidence suggests that, at least in the tetraphyllideans, small planktivorous fishes, such as the anchovy, serve as additional obligatory intermediate hosts between the crustacean and fish hosts (Overstreet, 1983). Cephalopods are thought to pick up post-larval stages by feeding on either crustaceans or small fishes. The cycle is completed when predaceous elasmobranchs feed on prey containing infective post-larvae.

Trypanorhynch post-larvae are not directly comparable to tetraphyllidean plerocercoids and hence some authors, such as Dollfus (1942), have proposed the term plerocercus for the equivalent life cycle stage. The term metacestode is used by many authors to refer to all post-larval stages between oncosphere and adult. Therefore, in the above discussions it would replace the words procercoid, pleurocercoid, and plerocercus.

In tetraphyllidean cestodes the scolex characteristically bears four large leaf-like flaps or bothridia. Plerocercoids of the genus *Phyllobothrium* occur free or attached in the stomach, caecum and rectum of host cephalopods. Though the genus was reviewed by Williams (1968), the species reported from cephalopods are not well known and the genus still needs extensive study. *Phyllobothrium loliginis* is the most common species encountered in cephalopods. Originally described by Leidy (1887) from *Illex illecebrosus*, this cestode has been reported in a number of species of loliginids (*Loligo*) and ommastrephids (*Illex*, *Todarodes*, *Todaropsis*) on both sides of the North Atlantic. Linton (1922b) and later Stunkard (1977) indicated that the species *P. tumidum* may be identical to *P. loliginis* in which case all host records may be referred to the one cestode species. (See also

Dollfus, 1936, 1958; Euzet, 1959; Guiart, 1933; Linton, 1922b; Squires, 1957; Stevensen, 1933; Stunkard, 1977).

In France, *Sepia officinalis* is infected by *Phyllobothrium lactua* (Dollfus, 1958). Two species originally placed in the genus *Orygmatobothrium* are now considered to belong to the genus *Phyllobothrium*. In the Mediterranean *Todarodes sagittatus* is infected with *P. dohrnii* and in the Baltic Sea *Eledone moschata* harbors *P. pusillus* (see Dollfus, 1936; Siebold, 1850). Specimens, referred to *Phyllobothrium*, but not identified to species, have been recovered from a wide diversity of hosts in addition to those listed above (see Brown & Threlfall, 1968a; Dollfus, 1958, 1964; Gayevskaya, 1977, 1977a, 1978; Gayevskaya & Nigmatulin, 1975, 1978; MacGinitie & MacGinitie, 1968; Naydenova & Zuev, 1978; Threlfall, 1970).

Representatives of the genus *Dinobothrium* have been reported from a few species of squids in the Mediterranean and on both sides of the Atlantic Ocean. Stunkard (1977) found *D. septaria* embedded in the digestive tract of *Loligo pealei. Illex, Todaropsis* and *Sepia* harbor either *D. plicitum* or an as yet undesignated species of *Dinobothrium* (see Brown & Threlfall, 1968a; Dollfus, 1936, 1958, 1964; Gayevskaya & Nigmatulin, 1975, 1978; Squires, 1957). Stunkard (1977) indicated the strong possibility that *D. septaria* and *D. plicitum* are conspecific. Evidence suggests that squids, especially the ommastrephids, may be obligate and not paratenic intermediate hosts for the dinobothrids which mature in large, oceanic selacians such as *Cetorhinus* and *Carcharodon*.

The genus *Pelichnibothrium* is represented by two species, though some workers (Yamaguti, 1959) consider the genus to be monotypic. Originally described from California by Riser (1949, 1956) *P. speciosum* and *P. caudatum* occur in *Dosidicus gigas* and *Loligo opalescens* respectively. *Pelichnibothrium speciosum* has also been recovered off Japan in *Loligo* (Yamaguti, 1934), off Newfoundland in *Illex illecebrosus* (Brown & Threlfall, 1968a), and off Argentina in *I. argentinus* (Threlfall, 1970). Adult worms have been recovered from the Blue Shark, *Prionace glauca*, the Opah, *Lampris regia*, and the Bluefin Tuna, *Thunnis thynnis* (see Yamaguti, 1934). Larval stages have been recently reported from the euphausiid, *Thysanoessa longipes* off Japan (Shimazu, 1975).

Loligo vulgaris is known to harbor two larval cestodes. *Diplobothrium pruvoti*, described by Guiart (1933) and later reclassified by Dollfus (1936) and placed in the genus *Scyphophyllidium*. According to Dollfus (1958) the true identity of the second species, originally named *Bothriocephalus loliginis* by Delle Chiaje (1829), is still an enigma.

The genus '*Scolex*' is a heterogenous assemblage in which tetraphyllidean plerocercoids of uncertain affinity are placed. Several distinct types of '*Scolex*' larvae have been described from some 30 species of decapods and octopods but most cannot be assigned to a specific genus or species (Dollfus, 1964). Wagener's '*Scolex bothriis bilocularis*' was found in *Loligo pealei* by Stunkard (1977) and tentatively identified as *Ceratobothrium xanthocephalum*. Adults infect the spiral valve of sharks such as *Galeocerdo*, *Lamna* and *Isurus*. The name '*S. pleuronectis*' represents a complex of species the members of which probably belong to either the genus *Phyllobothrium* or *Acanthobothrium* (Cake, 1976). Depending on the number of suckers in the bothridia, subspecific types have been designated as '*unilocularis*, *bilocularis*, *trilocularis* or *quadrilocularis*'. Other unidentified tetrephyllidean larvae are refered to by the name '*S. polymorphus*' or simply '*Scolex* sp.'. The literature in this area is confused and since descriptions of various larval forms are often inadequate, I have not made an attempt to identify specific hosts. However, even if the literature was consistent and complete descriptions were provided in the majority of cases, it would not be possible to identify the cestodes and relate them to specific cephalopod hosts. In all cases life history studies are critically needed. For additional information see Brown & Threllfall (1968a); Cake (1976); Dollfus (1923b; 1958, 1964); Euzet (1959); Gayevskaya & Nigmatulin (1975, 1978); Naydenova & Zuev (1978) and Stunkard (1977).

Cestodes in the Order Trypanorhynchidea

possess four tentacles armed with hooks and thus are easily identified. Larval stages are typically embedded in tough, fibrous cysts in the walls of the stomach and caecum of cephalopod hosts. Cephalopods appear to function merely as paratenic hosts, acquiring larval trypanorhynchs by feeding directly on euphausiids and other crustaceans or on teleost fishes, which also commonly serve as hosts. Trypanorhynchs mature only in the intestine of elasmobranch fishes.

The widely distributed genus *Nybelinia* is the most commonly encountered trypanorhynch in cephalopods. *Nybelinia lingualis* has been reported from a diversity of hosts in the Mediterranean, Atlantic and Indian Oceans, namely: *Sepia officinalis*, *Loligo vulgaris*, *Ommastrephes bartrami*, *O. pteropus*, *Symplectoteuthis oualaniensis*, *Eledone moschata*, and *Octopus vulgaris* (see Belyaeva, 1979; Cuenot, 1927; Dollfus, 1929, 1936, 1958, 1964: Gayevskaya, 1976; Gayevskaya & Nigmatulin, 1976b; Naydenova & Zuev, 1978; Pinter, 1930). *Loligo pealei* harbors both *N. bisulcata* and *N. yamagutii*. The latter species is also found in *Ommastrephes pteropus* and *Illex coindetti* (see Gayevskaya, 1977a; Gayevskaya & Nigmatulin, 1975, 1978; Stunkard, 1977). Off Japan, the prevalence of *N. surmenicola* in *Todarodes pacificus* may reach 22% (Dollfus, 1929, 1930, 1942; Kurochin, 1972; Yamaguti, 1934).

A number of undetermined or undescribed species of *Nybelinia* have been reported from *Sepiella*, *Lepidoteuthis*, *Moroteuthis*, *Illex*, *Notodarus*, *Ommastrephes*, *Symplectoteuthis* and *Gonatus* (see Belyaeva, 1979; Brown & Threlfall, 1968a; Clarke & Maul, 1962; Gayevskaya, 1977a; Gayevskaya & Nigmatulin, 1978; Hochberg, unpub.; Riser, 1949; Smith *et al.*, 1981; Yamaguti, 1934). Off Hawaii, I have commonly encountered two forms of *Nybelinia* in pelagic squids (Hochberg, unpub.). The first type is typically embedded in the digestive tracts of *Abralia*, *Abraliopsis*, *Enoploteuthis*, *Octopoteuthis*, *Histioteuthis*, *Symplectoteuthis*, and *Liocranchia*. The second type is found embedded either in the digestive gland or in the ventral mantle musculature of the sepiolid, *Heteroteuthis*. The older literature mentions *Amphistoma loliginis* and *Fasciola barbata* (=*F. loliginis*) from *Loligo vulgaris*. In both cases these worms are probably *N. lingualis* (see Dollfus, 1942, 1958).

A diversity of other genera of trypanorhynchs are known from cephalopods. Stunkard (1977) provisionally identified *Lacistorhynchus tenue* and *Otobothrium crenacolle* from *Loligo pealei*. *Tentacularia coryphaenae* has been recovered from a number of species of *Illex*, *Ommastrephes*, *Symplectoteuthis*, and *Todarodes* and from the finned octopod, *Chunioteuthis* (see Belyaeva, 1979; Dollfus, 1967; Gayevskaya, 1976, 1977a; Gayevskaya & Nigmatulin, 1976b, 1978; Naydenova & Zuev, 1978; Threlfall, *et al.*, 1971). Van Beneden (1870) mentioned finding a post-larva of *Christianelle minuta* in *Sepia officinalis*, though Dollfus (1958) doubts the validity of this earlier identification. *Dibothriorhynchus todari*, originally described by Delle Chiaje (1829, 1841) from *Todarodes sagittatus* was transferred to the genus *Hepatoxylon* by Yamaguti (1959). A second species of *Hepatoxylon*, *H. trichiuri*, has been reported from *Ommastrephes pteropus* in the Atlantic and from a specimen of *Architeuthis dux* stranded in Newfoundland (Gayevskaya, 1977a; Pippy & Aldrich, 1969).

Octopods generally harbor a distinct assemblage of trypanorhynch genera. Riser (1949, in Dollfus, 1964) identified a specimen of *Eutetrarhynchus* from *Octopus bimaculatus* in California. In France and Italy, *O. vulgaris* harbor both *Tetrabothriorhynchus octopodiae* and *Tetrarhynchus megabothrium* (see Diesing, 1850; Mingazzini, 1904; Redi, 1684; Vaullegeard, 1899). According to Dollfus (1958), this latter worm may represent a species of *Nybelinia*. Adam (1938) figured a *Nybelinia* from an unidentified octopus taken off the Andaman Islands in the Indian Ocean.

IX. ACANTHOCEPHALA

Two species of acanthocephalans have been reported from cephalopods. The presence of acanthocephalans in cephalopods is unusual since adults of this entirely parasitic phylum typically infect only vertebrate hosts. Gayevskaya (1977a) described and figured *Neorhadinorhynchus atlanticus* from the stomachs of *Om-*

mastrephes pteropus captured in the south Atlantic. Similar forms have also been recovered from the same host in the central and north Atlantic (Hochberg, unpub.; Naydenova & Zuev, 1978). Since these small (8-12 mm) rhadinorhynchids attain sexual maturity in cephalopods, Gayevskaya proposed that *O. pteropus* may function as a final host in this case and not simply a paratenic or transfer host. In the developmental cycle of acanthocephalans, stages normally infective to fishes are found in crustaceans and hence could also be ingested by squids.

Gayevskaya (1977a) and later Naydenova & Zuev (1978) referred to a second species, which also is found in *O. pteropus*, but which was located in the mantle cavity. Sufficient material was not available for identification of these large worms. Biological and ecological information relating to both parasites is not available.

X. NEMATODA

Larval nematodes are commonly encountered in many species of cuttlefishes, squids and octopuses. However, little information is available other than records of presence or absence. The abundant literature is complicated by a variety of unresolved taxonomic and nomenclatural problems (Smith & Wootten, 1978). In fact, the larval nematodes of marine animals, both fishes and invertebrates, are in need of critical review.

In the older cephalopod/parasite literature several species are briefly mentioned or figured. For the most part these worms are inadequately described and hence, a modern taxonomic designation cannot be applied. However, it is of interest to list these worms because the hosts are known and future investigators may some day be able to re-examine the host cephalopods and fit the pieces of the puzzle together.

Ascaris todari was reported to occur in *Ommastrephes bartrami* and *Todarodes sagittatus* in Naples (Delle Chiaje, 1829; Schuurmans-Stekhoven, 1935). A second species, *A. moschata*, was described by Stossich (1897; see Dollfus, 1958) from *Eledone moschata*, also from Italy. *Filaria loliginis* was described by Delle Chiaje (1829) from *Loligo vulgaris* captured in the vicinity of Naples. Schuurmans-Stekhoven (1935) indicated that the same nematode was found by Grümpe in the mantle cavity and ovaries of *Alloteuthis subulata* in Helgoland. Wülker (1930) presumed this worm to be a larval ascaridoid. Dujardin (1845) mentioned the presence of *F. piscium* in *Sepia officinalis*. This is probably the same nematode that Gros (1847) observed encysted in the stomach lining of *Sepia* (see Dollfus, 1958).

The majority of the nematodes that have been identified are ascaridoids. Five genera are reported to occur in cephalopods: *Porrocaecum* (Family Ascaridae); *Anisakis*, *Contracaecum*, *Terranova*, and *Hysterothylacium* (= *Thynnascaris*) (Family Anisakidae). Species in groups other than ascaridoids have been observed in cephalopods, but not commonly and they have not been reported. The only non-ascaridoid nematode reported from a cephalopod was an unidentified philometroid taken from the coelomic washings of *Loligo opalescens* in California (Dailey, 1969).

Although nematode genera are relatively easy to distinguish only a few species have been positively determined. In the Atlantic *Todarodes angolensis* and *Illex coindeti* only occasionally harbor *Porrocaecum* (Type I) larvae, whereas, a high percentage of *Ommastrephes bartrami* and *O. pteropus* were infected with *Porrocaecum* in both the North and South Atlantic (see Gayevskaya, 1974, 1976, 1977a; Gayevskaya & Nigmatulin, 1975, 1976a,b, 1978; Naydenova & Zuev, 1978). Belyaeva (1979) found *Porrocaecum* (Type I) larvae in *O. bartrami* in the Indian Ocean. 75-95% of the ommastrephids examined had small (3-5 mm), transparent larvae (Type I) encysted in connective tissue capsules on the external walls of the stomach, while 30-50% had larger worms (20-30 mm) encysted in the internal wall of the mantle. These worms are considered to be the same species, and they are characteristic of oceanic hosts.

In Norway, Berland (1961) was the first to note the presence of *Anisakis simplex*, encysted in the ventricle of *Todarodes sagittatus* (see Pippy & Banning, 1975). Throughout Japan, third stage larval anisakids of two distinct species have been commonly recovered by a

number of investigators from *T. pacificus* and more rarely from *Doryteuthis bleekeri* (Kagei, 1970; Kato, *et al.*, 1968; Kobayashi, *et al.*, 1966; Koga, *et al.*, 1968; Kosugi, *et al.*, 1969; Koyama, *et al.*, 1969; Kurochin, 1972; Oishi, *et al.*, 1969; Okumura, 1967; Orihara, *et al.*, 1968; Oshima, 1972). A number of other species of cephalopods have been examined in the Orient and all have been found to be negative. Type I larvae are probably *A. simplex* and Type II larvae are currently recognised as *A. physeteris*. The majority of these worms occurred in circular cysts in the secretory portions of the visceral organs, and in the lining of the mantle cavity, although many also were found in the mantle musculature. When *Todarodes* makes a northward migration along the coast of Japan in spring and summer, the prevalence of infection is low, generally less than 10%. As the squid migrate southward during the fall and winter, following their stay in the waters off Hokkaido, the prevalence of nematodes rises to over 70% (Oshima, 1972). Their diet at this time is principally euphausiids which are known to harbor larval anisakids (Oshima, *et al.*, 1969; Shimazu & Oshima, 1972; Smith, 1971). Off New Zealand, *A. simplex* larvae have been found in a complex of *Notodarus* species (Smith, *et al.*, 1981).

Anisakis larvae have been observed by Clarke & Maul (1962) in a specimen of *Lepidoteuthis grimaldi* captured in the Atlantic and by Threlfall (1970) in *Illex argentinus* off Mar del Plata, Argentina. Belyaeva (1979) recovered *Anisakis* (Type I) larvae in *Symplectoteuthis* and *Ommastrephes* in the Indian Ocean. Gayevskaya & Nigmatulin (1975) reported *Anisakis* (Type I) larvae in *Todaropsis eblane* and *Todarodes angolensis* off southwest Africa and *O. pteropus* in several areas of the Atlantic. *Anisakis* (Type II) larvae occurred in 2% of the *O. bartrami* examined in the Atlantic by Gayevskaya. Normally, only one large (20 mm), pink worm occurred per host, in the lumen of the ovary or testis (Gayevskaya, 1976).

Terranova larvae are rarely found in squids off Japan (Orihara, *et al.*, 1968; Oshima, 1972). However, *Contracaecum* (Type B) larvae are commonly noted in the muscles of *Todarodes pacificus* (see Kikuchi, *et al.*, 1969, 1972; Kosugi, *et al.*, 1970; Oshima, 1972; Shiraki, 1969, 1974). In their review, Norris & Overstreet (1976) indicated that this latter worm represented a member of the genus *Thynnascaris*, whereas Deardorff & Overstreet (1981) transferred it to the genus *Hysterothylacium*. Both publications list *H. reliquens* as occurring in *Lolliguncula brevis* off Mississippi in the Gulf of Mexico. Brunsdon (1956) found *Contracaecum* larvae in the stomach and mesenteries of *Nototodarus sloani* off New Zealand but a positive identification has not been made (Hurst, pers. comm.). Cannon (1977) remarks that *Anisakis* and *Terranova* are typically found in plankton and nekton feeders, whereas *Contracaecum* and *Thynnascaris* occur principally in bottom feeders. In general this fits with the feeding habits of the cephalopods listed above but would be worthy of further investigation.

Unidentified nematodes have been recovered on numerous occasions from cephalopods. Nouvel, working in Monaco, found nematodes encysted in the mantle of *Onychoteuthis banksi* and *Sepia orbignyana*, in the stomach of *S. elegans*, and in the rectum of *Sepiola atlantica* and *Eledone aldrovandi* (see Dollfus, 1958). In France, Dollfus recovered nematodes from the musculature of *Histioteuthis bonelliana* and from the stomach of *Illex coindeti*. Off California and Hawaii, I have observed larval nematodes encysted in the digestive tracts of oceanic squids such as *Abralia*, *Abraliopsis*, *Enoploteuthis*, *Pterygioteuthis*, *Moroteuthis*, *Symplectoteuthis*, *Chiroteuthis*, *Japatella*, and *Vampyroteuthis*. In the Gulf of California, Mexico, I observed *Loliolopsis diomedeae* to be heavily infected with larval nematodes.

Oshima (1972) reviewed the life cycle of *Anisakis*. Adult worms are present in the stomachs of many cetaceans, especially the small toothed whales, and a few pinnipeds. Embryonated eggs are shed to the exterior with the feces. Following a single molt within the egg, ensheathed second stage larvae emerge in the sea water. The larvae are preyed upon by euphausiid crustaceans. Upon ingestion, the larval nematodes migrate into the hemocoel of the crustacean. Third stage larvae develop

following exsheathment and another molt in the hemocoel of the first intermediate host. The prevalence of infection in euphausiids is very low but fishes and squids concentrate larvae as they feed on many hundreds or thousands of euphausiids during their life time. In these second intermediate hosts, the third stage larvae penetrate the alimentary tract and encyst in the organs of the body cavity or in the muscles. Advanced third stage larvae can be serially passed through the oceanic food chain without additional molts occurring. This further concentrates the larvae in a wide diversity of predatory fishes. Squids probably function as obligatory paratenic or transport hosts in the cycle. The cycle is completed when third stage larvae are consumed by marine mammals. Attaching to the stomach wall, the nematodes undergo two more molts, grow and eventually develop into sexually mature adults.

In certain areas of the world such as Japan, Korea, California, Britain, and Scandinavia, where uncooked fishes and squids are eaten anisakiasis is an important human health problem (See Cheng, 1976; Myers, 1975; Oishi, *et al.*, 1969; Okumura, 1967; Oshima, 1966, 1972; Smith & Wootten, 1978; Williams & Jones, 1976). Human infections, attributed to larval ascaridoid nematodes, are characterized by small ulcers or lesions, particularly in the stomach. This disease is typically transmitted through fishes, though squids, especially *Todarodes pacificus*, serve an equally important role (see Doi, 1973; Okumura, 1967; Oshima, 1972). Experimental evidence is lacking to positively link the larval nematodes in cephalopods with pathological symptoms in man, but most clinical parasitologists hold the opinion that species of larval anisakids, normally infective to marine mammal or bird final hosts, may be infective to humans if they ingest raw or partially cooked squids. The numerous reports of larval ascaridoids makes this an area of potential concern especially when considering the increased harvest of squids throughout the world.

XI. ANNELIDA

A. Hirudinea

Three species of hirudineans have been recovered from cephalopods, in all cases from *Octopus dofleini*. All are piscicolids which have very small posterior suckers and commonly attach to arthropods. Leeches normally obtain blood meals from fishes although some species have been reported to feed on crustaceans. Many of the species which feed on fishes eventually leave to deposit cocoons on hard shelled invertebrates such as crustaceans, pycnogonids, and bivalves (Overstreet, 1983). The association with octopuses appears to be temporary and may or may not involve feeding. Transfer most likely occurs when cephalopods feed on crustaceans.

Borovitzkaya (1949) described *Crangonobdella achmerovi* from *Octopus dofleini* captured in the Okhotsk Sea. According to Epshtein (1962) this species is synonymous with *C. murmanica* which parasitizes the shrimp, *Sclerocrangon*, and the fish, *Myoxocephalus*. The worm is widely distributed in Arctic waters having been reported in Greenland, Alaska and Russia as well as in the Okhotsk and Bering Sea. A second species, *Osterobdella papillata* was described and figured by Burreson (1977) from *O. dofleini* collected off Oregon. A species identified as *Johanssonia arctica* (Burreson, pers. comm.) has been found on *O. dofleini* off California. This latter species commonly attaches to deep sea pycnogonids (i.e., *Nymphon* and *Colossendeis*) and decapod crustaceans (i.e., *Chionoecetes*, *Paralithodes*, and *Hyas*) and is also reported to infest fishes (i.e., *Anarhichas* and *Gadus*). *Johanssonia arctica* is circumpolar in description, occurring throughout the Arctic Ocean, as far south as Newfoundland in the western Atlantic Ocean, and as far south as California in the eastern Pacific Ocean. See Meyer & Khan (1979) for a review of this species.

B. Polychaeta

Polychaetes are not commonly recognized as symbionts of cephalopods. Clark (1956) and Cheng (1967) reviewed the polychaete annelids which live in the gelatinous egg masses of neritic loliginid squids. *Capitella capitata ovincola* was described from the egg fingers of *Loligo opalescens* off California (Hartman, 1947, 1961). Hartman (1959) later described a

second subspecies, *C. c. floridana*, obtained from the eggs of an unidentified squid collected off Florida. In France, the egg masses of *Loligo vulgaris* harbor two additional species. Boletzky & Dohle (1967) named *C. hermaphrodita* and Harant & Jecklins (1933) identified *Capitomastus minimus*.

At present these small capitellids are known only from the benthic egg masses of *Loligo*. They have not been encountered in the egg masses of any other cephalopod genera. All the worms live in mucoid tubes which irregularly penetrate the capsular matrix of the squid egg masses. Harant & Jecklins (1933) postulated that *Capitomastus* secretes an enzyme which dissolves the capsular membranes of the squid eggs and makes them suitable for food. *Capitella*, on the other hand, feeds only on the jelly in which the eggs are embedded and apparently does not harm the developing embryos. In the case of *C. c. ovincola*, the worms infest the egg masses at the time they are laid on the bottom. The worms become sexually mature and reproduce about the time the squids hatch (see Fields, 1950, 1965; MacGinitie & MacGinitie, 1968; McGowan, 1954). Though these capitellids are most similar to micropredators and not parasites, the degree of host and substrate specificity and the nature of the synchrony of life histories indicate a complex and highly specialized symbiotic interaction.

XII. ARTHROPODA/CRUSTACEA

Few published reports treat the crustaceans associated with cephalopods. Ten copepods, one branchiuran and three isopods have been described. These occur principally in the mantle cavity and on the gills of their cephalopod hosts. Other potential parasitic arthropods, such as mites and pycnogonids, and crustaceans, such as barnacles and amphipods are not known to infect cephalopods. For reviews see Dollfus (1958), Monod & Dollfus (1932), and Pelseneer (1929).

A. Copepoda

The copepods associated with cephalopods do not form a systematic unity. The majority of species have been classified with the poecilostomatoids but siphonostomatoids and harpacticoids are also represented. Most of the species are commensals and not true parasites (i.e., they do not injure the host) though in the majority of cases the relationships are highly host specific.

Members of two genera of siphonostomatoid copepods are reported from cephalopods. Tiny 'tad-pole like creatures' originally discovered by Smith (1887) on *Nautilus*, are now known to be caligid copepods of the genus *Anchicaligus*. Ho (1980) recently redescribed the single species, *A. nautili*, which had not been studied in detail since the time of Stebbing (1900). *Anchicaligus nautilii* is the only caligid known to parasitize a deep-water molluscan host. All the nearly 400 other species in the family infect coastal or oceanic fishes. The copepod infects *N. pompilius* and probably *N. macromphalus*. It is distributed throughout the range of both hosts in the Indo-Pacific. Little is known about the biology of the copepod. In his letters from New Guinea, Wiley (1896) reported that *A. nautili* attaches to the gills and moves around in the mantle cavity. Haven (1972) indicated that the 'commensal copepod' was common inside the funnel and on the inner surfaces of the ala infundibulae of *N. pompilius* in the Philippines. Wiley and others have noted that when nautiluses are placed in containers of water, the copepods emerge in large numbers from the mantle cavity and actively swim about. Although not completely known for *A. nautili*, the life cycle of some caligid copepods involves an intermediate host to which a series of chalimus larval stages are attached.

Larval stages of the pennellid '*Pennella varians*' have been repeatedly noted on the gills of *Eledone moschata*, *Sepia officinalis*, *S. elegans*, *Loligo vulgaris* and *Todaropsis eblane* (see Rose & Hamon, 1953; Rose & Vaissiere, 1953; and Wierzejski, 1877). All published reports indicate that only cephalopods from the Mediterranean are infected with this siphonostomatoid copepod. Originally described by Steenstrup & Lütken (1861), adults of this parasite typically occur on a variety of fishes. The presence of *Pennella* on cephalopods has been contested by Stock (1960). However, a specimen which I recovered from the gills of *Alloteuthis subulata* off Plymouth, England,

was recently identified as a male *Pennella* (Ho, pers. comm.).

Two species of harpacticoid copepods in the tisbid genus, *Cholidya*, are known from the deep benthic octopods. Faran (1914) described *C. polypi* from specimens taken off the inner surface of the arm web of *Benthoctopus ergasticus* (= *Polypus profundicola*). The host was captured off the coast of Iceland. Bresciani (1970) described *C. intermedia* from an unidentified cirroteuthid collected off Britain in the Channel between the Faroe and Shetland Islands. This latter species occurred in the mantle cavity and on the gills. Nothing is known about the biology or life history of either copopod species.

The lichmologids are highly mobile poecilostomatoid copepods which actively move about over the suface of invertebrate hosts feeding on mucus. In their review of the family, Humes & Stock (1973) discussed the species known to live on cephalopods. *Lichomolgus longicauda* (= *Sepicola longicauda* and *L. sepicola*), is found on the gills and in the mantle cavity of *Sepia officinalis* and *S. filliouxi* wherever these two species of cuttlefishes occur (see Claus, 1960; Cuenot, 1927; Pesta, 1909; Stock, 1956, 1960; Wiezejski, 1877). Ho (pers. comm.) considers the copepod to belong to the genus *Doridicola* and not *Lichomolgus*. Another species of *Doridicola*, *D. sepiae* (= *Lichomolgus sepiae*), was reported by Izawa (1976) from *Sepia esculenta* in Japan. Stock (1960, 1964) recovered a single specimen of *Doridicola* ? *agilis* from the gills of *Todarodes sagittatus* at Rosas, Spain.

Members of the genus *Octopicola* live in specific association with octopuses. In the English Channel and in the Mediterranean *Octopus vulgaris* is infected with *O. superbus superbus*. In the West Indies, at Barbados and Curaçao, the same species (?) of host harbors *O. s. antillensis*. Humes & Stock (1973) identified the latter subspecies from *Octopus briareus* collected at several sites in Florida. *Octopus cyaneus* captured off Madagascar were infested with *O. stocki*, whereas *O. regalis* was present in the same host in the Pacific Ocean at New Caledonia and Eniwetok Atoll. For additional details on descriptions and distributions see: Bocquet & Stock (1960); Delamare Deboutteville, *et al.* (1975); Humes (1957, 1963, 1974); Humes & Stock (1972); and Stock, *et al.* (1963).

These small, cyclopiform copepods normally live in the mantle cavities of their octopus hosts though they may also be found on the body surfaces and amongst the eggs. In the mantle cavity they move about freely over the gills or attach, by means of the second antennae, to the arterial stems beneath the branchial leaflets. No damage to the tissues of the gills or the mantle cavities has been reported. Delamare Deboutteville, *et al.* (1957) noted that the European species, *O. superbus*, inhabits the mantle cavity during the day but moves out on the arms and over the head and mantle after dark.

All lichomolgids have a single host life cycle. Delamare Deboutteville and coworkers demonstrated that *Octopicola* exhibits a strong chemotaxis to the egg masses of the octopus. They are probably correct in assuming that autoinfestation regularly takes place. Gotto (1962) suggested that the reproductive rates of lichomolgids (i.e. egg number) reflects the mobility and habits of the host. He compared *Doridicola* (= *Lichomolgus*) which infects the cuttlefish, *Sepia*, and has a high egg count, with *Octopicola* which occurs in association with the more sedentary *Octopus* and produces a much smaller number of eggs.

B. *Branchiura*

The branchiurans are small copepod-like crustaceans which are external parasites of teleost fishes. However, a single species, *Argulus arcassonensis*, lives on the skin of *Sepia fillìouxi*. It has, thus far, only been reported from Arcachon, France (see Argilas, 1936; Ceunot, 1912, 1927). Like other ectoparasitic crustaceans this species is dorsoventrally flattened and has developed modifications to enhance the efficiency of attachment and feeding. The second maxillae are greatly enlarged and modified as suckers to aid in attaching to the skin of the host and the mouth parts are adapted for piercing and sucking the blood and body fluids of the host.

C. *Malacostraca*

Of the parasitic malacostracans only a few

isopods have been discovered on cephalopods. Though rare, they occur principally in the mantle cavity. *'Aegathoa occulata'* (=*A. loliginea*) infests *Loligo pealei* as well as a number of species of fishes found along the Atlantic and Gulf coast of the United States, Mexico and the West Indies (see Harger, 1878; Richardson, 1905). However, additional study is needed since the genus *Aegathoa* is considered to be a group name which represents a complex of young isopods of several genera and species. A second species, *Nerocila orbignyi*, was collected by Szidat (1955) from *Loligo* off the coast of Argentina. A single individual of an undetermined species of *Codonophilus* (=*Meinertia*) was taken by Dollfus (1958) from a specimen of *Sepia elegans* captured at Port-Vendres, France. And, a single individual of an unidentified isopod has been recovered from *Abraliopsis felis* in the North Pacific.

All the isopods named above are cymothoids, which as adults typically inhabit the gill chambers, skin and fins of fishes. Narrow host specificity is generally not observed, since these parasites are not permanently attached. Sexual dimorphism is the rule and the life cycle is protandric. Males are similar in size and shape to juveniles whereas females are very much larger and their bodies asymmetrically proportioned. Female isopods brood their eggs in a special marsupium under the thorax. Following hatching a free-swimming, manca stage is released. During juvenile development, the aegathoid stage attaches to a fish or cephalopod host. After settling on the host adult male characters are attained with the next molt. The male phase continues through several additional molts until a second individual lands on the host. At this point the larger of the two isopods is transformed into a functional female and begins to produce eggs. If the female dies, the male which remains begins to molt and eventually assumes the role of the female when another isopod settles on the host. For examples of cymothoid life cycles see Bowman (1960) and Brusca (1978).

In a few cases, brachyuran malacostracans have been reported as commensals in the mantle cavity of squids. Fischer (1943) found specimens of the galatheid, *Munida bamffia*, in the mantle cavity of *Alloteuthis subulata* being dissected by his students in Paris. Serene (1961) discovered megalopa larvae of an unknown crab in a number of *Loligo* captured off Viet Nam. On the surface these would appear to be 'accidental' associations, but Serene indicated that, in all cases, only one megalopa was found per host and that, in each case, the coloration blended perfectly with that of the host cephalopod.

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A REVIEW OF THE LABORATORY MAINTENANCE, REARING AND CULTURE OF CEPHALOPOD MOLLUSCS

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Abstract

The historical and current developments associated with keeping cephalopods in captivity are reviewed. While cephalopod maintenance is straightforward for many species, rearing and culture are still in the early stages of development and have been accomplished only on a relatively small scale, although recent advances have been substantial. A detailed review of cephalopod diets shows that cephalopods are active carnivores from hatching to adulthood and that they feed primarily on crustaceans, although shelled molluscs, fishes and other cephalopods also are consumed. To be maintained, reared or cultured successfully, they generally need: (1) careful handling to avoid skin damage, (2) tank space appropriate for their benthic or nektonic mode of life, (3) a good supply of high quality water, and (4) a sufficient supply of live food. Diseases in captivity in only a few cases have been a major problem. Culture is a useful means of providing animals as research models and of obtaining life cycle information, particularly that of the critical early developmental periods. A major economic impediment to large-scale culture is the development of a cheap, reliable artificial food.

Introduction

Previous reviews of cephalopod maintenance and culture have been provided by Grimpe (1928), Boletzky (1974a) and Shevtsova (1977). In view of the fact that there has been a resurgence in worldwide interest in cephalopods during the past few years, we present here an updated review that concentrates particularly on the diets of cephalopods as well as current advances in culture methodology and the future potential of culture programs.

What is to be learned from the culture of cephalopods? These dynamic predators occupy a dominant position in the trophic relationships of the marine ecosystem. They are an important food source for human consumption and they are unique and versatile research models. The first International Workshop on the Biology and Resource Potential of Cephalopods has clearly shown how little is known about their early life histories, recruitment into populations, predator-prey relationships and other facets of their life cycles. The scientific community is forced to depend largely upon culture programs to provide such information, especially on early life histories, because it is extremely difficult to make direct and detailed observations of cephalopods in nature due to their mobility, excellent vision and generally nocturnal habits. Culture programs also may become useful in providing selected species as biological models in experimentation, as for example the retina, the giant axon of the squid and the brain of the octopus. Culture therefore can be considered a means by which a number of pertinent problems of basic and applied science can be solved.

We have attempted to provide an overview as informative and detailed as possible, but inevitably there will be gaps and inaccuracies that escaped our attention. Nevertheless we hope that this article may prove useful as a source of information and stimulation to biologists and culturists interested in specific aspects of the 'indoor' biology of cephalopods.

A. Terminology

In reviewing the literature we found little uniformity in the use of terms that relate to culture. In an effort to standardize their usage, we follow the definitions introduced by Paffenhöfer and Harris (1979) for plankton culture, but we have modified them slightly so that they apply more specifically to cephalopods.

Maintenance: Holding wild-caught late juvenile or adult stages in the same approximate developmental stage for varying periods, with no direct intention of growing them to a more advanced stage (e.g., maintaining sexually mature adults until they lay eggs for rearing

studies, or holding wild-caught animals until needed for experiments).

Rearing: Growing a cephalopod over a certain period of time without achieving a second generation. Specifically it refers to any attempt to grow hatchlings or young juveniles to full size and sexual maturity.

Culture: Growing a cephalopod at least from hatching, through the complete life cycle (juvenile and adult stages, sexual maturity, mating and egg laying), to hatching of viable young of the first filial (F_1) generation. The term culture also may be used in the sense of collectively referring to maintenance, rearing and culture. These definitions do not apply to existing literature because terms often have been used interchangeably, especially the terms rearing and culture.

The standard measure of body size of cephalopods used throughout this paper is dorsal mantle length = ML.

The popular and scientific names of prey animals are given as quoted in the original papers.

B. HISTORICAL PERSPECTIVE

Cephalopods have a somewhat undeserved reputation for being delicate sea creatures that do not survive well in captivity. It is true that, among the approximately 700 species inhabiting all the world's oceans, a great majority would require specialized capture and maintenance techniques that cannot practically be provided. But there are many species living in the continental shelf waters of the world that thus far have proved fit for life in captivity and some of these hold great interest from the scientific perspective.

In a very detailed review with a translated title of 'Maintenance, handling and breeding cephalopods for zoological and physiological purposes', Grimpe (1928) presented the state of the art in cephalopod maintenance. He was particularly acquainted with these problems through years of experimental cephalopod research, mostly in the Zoological Station in Naples, Italy. Unfortunately, Grimpe's review marked the end of a period of very active cephalopod research. By the end of the 1920's only a handful of scientists remained who worked with living cephalopods. If the economic conditions had been more favorable then, cephalopod research and culture attempts quickly might have reached the state that was actually realized a full 30 years later. With the new drive of marine biology in the 1950's and 1960's, with possible applications in 'sea farming' or 'mariculture', it appeared to be a mere matter of time and technical improvement before large-scale cultures of cephalopods for human consumption would begin. Everyone now knows that this was unrealistic. Even now, most natural cephalopod stocks are so far from depletion that there is no sufficient market pressure towards alternative modes of cephalopod production.

Meanwhile, a different market opened and is expanding in the biological sciences. It comprises two sections: one for life cycle analyses, another for the production of cephalopods as experimental animals. The former is important for basic biological and ecological research as well as for fisheries biology dealing with cephalopod stocks, their exploitation and protection. The latter is important for many research projects in cell biology and neuroscience, in particular as a means of providing giant axons of squids all year long. The extent to which this market expands will set the pace of future culture work on cephalopods. The following chapters address technological limitations of culture faced by the culturist as well as biological limitations of culture imposed by the nature of cephalopods.

Collection Methods

The procurement of healthy eggs, juveniles or adults of marine animals for laboratory study often is difficult because collection and transportation procedures must be adapted to: (1) temperature and salinity requirements of each organism, and (2) the degree of stress that each species can tolerate from the trauma of capture, shipboard handling and transport, and transfer procedures into the laboratory tanks. These limitations are particularly strict with cephalopods that move very actively and tend to damage their integument. Recent reports by Leibovitz *et al.* (1977) and Hulet *et al.* (1979)

have described the consequences of skin damage in pelagic squids and they reemphasize the importance of developing atraumatic capture methods for squids and other cephalopods.

It is not within the scope of this review to list all the collection methods for cephalopods, but some techniques will be listed below for the three general stages that interest culturists. Some general reviews on collection techniques are given by Voss (1973), Zuev and Nesis (1971), FAO (1975) and Tomiyama and Hibiya (1978). These methods do not always emphasize the atraumatic capture of animals and therefore their use in obtaining healthy animals for laboratory study and breeding often is limited. Obtaining experimental animals from existing fisheries generally is the easiest and most inexpensive solution to collection, especially when it is not necessary to obtain animals in perfect condition. Slightly damaged animals often are able to spawn in the aquarium, and this allows one to take care of the egg masses from the beginning of embryonic development.

Eggs of species that spawn on open stretches of sandy or muddy bottom can be collected with bottom trawls, but care must be taken to limit the mechanical disturbance of the egg masses, especially when the net is taken onboard for sorting of the material and when temperatures rise during sorting on deck. These problems are more easily dealt with when eggs laid inshore (not deeper than 40-60 m) are collected by SCUBA diving, which in addition allows one to have access to rocky bottoms where trawling is impossible. Indeed, squid eggs often are deposited under rocky overhangs. In addition to this mode, Takeuchi (1969, 1976) has observed that *Doryteuthis bleekeri* spawns on the abdomen of the giant spider crab *Macrocheira kaempferi*. Eggs of some cuttlefishes and squids such as *Sepioteuthis lessoniana* may be collected by placing tree branches on spawning grounds to which females attach their eggs (Mangold-Wirz, 1963; Choe, 1966a; Tomiyama & Hibiya, 1978). For many species, it is easier first to obtain adult animals by trawling, maintain them in aquaria until spawning and then collect the eggs there. In loliginid squids and cuttlefishes, egg-laying can be triggered by certain visual stimuli, especially by natural or artificial egg masses placed in the aquarium (Arnold, 1962).

The collection of young juveniles generally is the most difficult undertaking. Even very small cephalopods are able to avoid most collecting gear, and if caught, they accrue considerable stress and injury to a degree that drastically limits their survival. The young of many species have more rigid feeding requirements than the adults, and the trauma of capture often upsets highly specific feeding responses. Lighted traps set at night probably would be the best collecting device for fragile cephalopod juveniles, but this technique has not been used frequently. Most of the cephalopod juveniles described in the literature have been captured with plankton nets and midwater trawls. Very small benthic sepioids, especially sepiolids, are regularly captured with a small sled-dredge used for various purposes by the Laboratoire Arago in Banyuls.

The collection of adult cephalopods is more straightforward but varies considerably for different ecological situations. Most cuttlefishes and sepiolids are collected by bottom trawl. When the duration of tows is limited (20 min. to 1 hr.) and net retrieval and sorting of catch are carried out carefully, a fair percentage of the captured sepioids survive with minimal skin damage. Many squids (loliginids and oegopsids) are caught routinely with bottom and midwater trawls, but a very small fraction of the catch avoids major skin and fin damage. This is not a very desirable collection method for most squid species if long-term maintenance is required (but see Hulet *et al.*, 1980 for successful trawl capture of *Lolliguncula brevis*). Collections by static pound nets (cf. O'Dor *et al.*, 1977 for *Illex illecebrosus*) or encirclement nets (e.g., purse seines, lampara nets) are good methods because the squids do not incur much net contact. Attraction to night lights and subsequent capture by dipnets or squid jigs is a favorable method of capture because the squids are nearly injury-free and the chances for survival are high. Some species, especially reef-dwelling loliginids, may be hand-collected during diving at night by mesmerizing individuals with bright lights. Octopods are most often caught with bottom trawls, but in many fisheries they are trapped in empty pots in which the animals seek

refuge (Lane, 1960; Inoue, 1969). Small benthic octopodids (members of the only benthic family—Octopodidae—within the Incirrata) may be collected by hand while SCUBA diving.

Atraumatic capture methods are of little use if the subsequent acclimation to laboratory conditions fails. This acclimation must be coupled with the transport procedure from the moment of capture. Transfer from water-to-air-to-water should be avoided or kept to a minimum, and particularly temperature, salinity, and pH of the water and lighting in holding tanks should be monitored in order to avoid physiological shock. Cephalopods generally need high quality water and adequate oxygenation. Recent investigations by commercial fish dealers show that many marine organisms transported in small volumes of water for long periods of time produce nitrogenous wastes that reach lethal levels and drop the pH before oxygen is depleted. Recent experiments carried out with squids at the Marine Biomedical Institute at Galveston show the same effect. It is important to provide an adequate volume of clean sea water for each animal *at all times*, beginning immediately after capture and continuing throughout the period the animals are kept in aquaria.

In general the culturist will have to judge the best collection and acclimation methods for a given species. Both availability and habits of cephalopods vary from one species to another, and consultation with local fishermen and scientists familiar with the desired species always is advisable.

General Culture Requirements

A. WATER QUALITY

The quality and quantity of sea water available to each animal represent the most essential aspects of culture. Cephalopods generally require fairly large quantities of clean, oxygenated sea water within a relatively narrow range of salinities. Unlike some of their sedentary molluscan relatives who can tolerate or shut out undesirable water, the cephalopods must rely on locomotion to avoid unsuitable water. In captivity they lose this option and the culturist must insure that water requirements are met at all times.

The most important parameters of water quality (but certainly not all) for consideration in culture are: temperature, salinity, pH, O_2, ammonia (NH_3), nitrite (NO_2) and nitrate (NO_3). In open systems usually only the temperature and salinity are likely to fluctuate, whereas in closed systems the remaining parameters are more likely to fluctuate. Because food items decompose and the cephalopods excrete nitrogenous wastes, especially the levels of toxic ammonia, nitrite and nitrate must be monitored most carefully. No tolerance levels have been clearly established for cephalopods. Temperature tolerances are species-specific and range widely, but salinity tolerances are more restrictive since most cephalopods are stenohaline (except *Lolliguncula* spp., cf. Hendrix *et al.*, 1981). Still, most species lie within the range of 27 to 38 ppt. The range for pH is restricted to that of sea water, usually 7.7 to 8.2. Dissolved oxygen levels always should be near saturation, particularly for the active, pelagic teuthoids, although some benthic octopods are surprisingly tolerant of low oxygen levels. For example, Maginniss and Wells (1969) found that *O. cyanea* did not show signs of distress until oxygen levels fell to 0.6 mg/l, only 11% of saturation levels. The limits for nitrogenous waste levels should follow those proposed by Spotte (1979) for most marine animals: <0.10 mg/l ammonia, <0.10 mg/l nitrite and <20.00 mg/l nitrate. The tolerance limits for some species certainly are above these figures. Vevers (1962) reported that *Octopus vulgaris* lived for nine months, mated and laid viable eggs in a closed system with levels up to 10 mg/l nitrate. Hirayama (1966) found that *Octopus vulgaris* withstood 1400 mg/l nitrate for ten hours before dying. Forsythe and Hanlon (1980) found that *O. joubini* tolerated 150 mg/l nitrate for several days with no adverse effects, and Hanlon and Forsythe (unpublished data) determined the 96 hour medium tolerance limit of *Octopus joubini* hatchlings to be near 15 mg/l nitrite, a level far higher than anticipated. In closed systems it is highly recommended that accurate colorimetric methods be used periodically to monitor levels

of ammonia, nitrite and nitrate (see methods in Rand *et al.*, 1976; Spotte, 1979; Strickland & Parsons, 1972).

The exact quantity of sea water needed per individual cephalopod is unknown. In open, or flow-through, systems one need only regulate the flow rate through the rearing chamber to insure that used sea water is constantly replaced. But in closed, recirculating systems both the volume and the flow rate are important. Presently it is not possible to define specific volume requirements for various developmental stages of most species. It is always better to have a larger volume system than anticipated, first because large-volume systems are more biologically stable, and second because there is a better chance that each individual cephalopod will receive its minimum volume of water for life functions. Estimates of water volume/animal can be empirically derived only and will come with refinement of culture technology. For example, Forsythe and Hanlon (1980, 1981) were able to rear 56 *O. joubini* to sexual maturity (mean wet weight 14 g each at 23 weeks) in a 300 l closed system. This works out to roughly 5.4 l of water per octopus, or 0.38 l of water per g of octopus. These figures depend entirely upon the filtration system employed and certainly the minimum amount of water needed per *O. joubini* is less than this. Behavioural parameters concerning aggression and territoriality in some species of cephalopods will determine the volume of water/animal, in addition to filtration capacity of the system.

Both natural and artificial sea water are acceptable media for nearly all aspects of cephalopod cultures. The vast majority of work has been done with natural sea water, but much recent work has shown that artificial sea salts are at least adequate, if not superior in some ways. At The Marine Biomedical Institute in Galveston, Hanlon and his co-workers have maintained or reared ten species of cephalopods in artificial sea water, and workers elsewhere have had similar success. While much definitive analysis remains to be done on the efficacy of artificial sea salt composition, especially with respect to replenishment of trace elemenents, it is sufficiently safe at this time to state that it is a suitable medium.

B. TANK SYSTEMS

The essential requirements of a seawater system are that it deliver adequate clean water to every individual and that it provide sufficient horizontal and vertical space to accommodate the feeding, locomotory and other behavioural habits of the species. Theoretically the system should be a facsimile of the animal's natural environment, but in practice this is not feasible, and in fact cephalopods often are sufficiently adaptable that they will live and grow in relatively crude imitations of their habitat.

One of the first considerations in culture work is whether to use an open or closed seawater system, but this will probably be a straightforward decision based upon the researcher's access to natural sea water. It becomes a purely technical and economical consideration, because from the biological point of view the animal needs only water of high quality, irrespective of its delivery system. Open systems are proven, reliable and convenient, but they require a coastal location with high water quality, and they offer little or no control over temperature and salinity fluctuations, disease organisms, turbidity and pollutants. Closed systems provide a stable, controllable and reproducible marine environment and, with the use of artificial sea water, can be operated in any locale. But they require fairly high initial cost and more care in maintaining a good biological balance.

Tables 1 and 2 are a compilation of cephalopod species maintained, reared or cultured in open or closed systems. It is noteworthy that most of the closed system work is recent, and this partially reflects an increase in the understanding and implementation of the closed system approach used by many large inland public aquaria. One of the earliest successful culture experiments with *Sepia officinalis* was carried out in the closed system of the Berlin Aquarium (Schröder, 1966), and there are several public aquaria worldwide that commonly maintain *Nautilus*, *Sepia*, and *Octopus* for public viewing.

Filtration design and efficiency are critical elements in open or closed systems. Submerged filters composed of sand, gravel (usually crushed oyster shell, dolomite, or 'lavalite'

TABLE 1

Open Seawater System Rearing or Maintenance of Cephalopods. This is a partial literature review with representative citations for each species listed in alphabetical order. Asterisk indicates species with benthic young.

Subclass NAUTILOIDEA (nautilus)	
Nautilus macromphalus	Bidder, 1962; Cousteau, 1971; Haven, 1972; Martin *et al.*, 1978
Subclass COLEOIDEA	
Order Sepioidea (cuttlefishes)	
Family Sepiidae	
**Sepia esculenta*	Choe, 1966a,b
**Sepia subaculeata*	Choe and Oshima, 1963
**Sepia maindroni*	
**Sepia latimanus*	Inoha, 1971
**Sepia officinalis*	Boletzky, 1974b and 1979b; Dendton & Gilpin-Brown, 1973; Féral, 1977, 1978; Pascual, 1978; Richard, 1966, 1975; Yim & Boucaud-Camou, 1980
**Sepia lycidas*	Fukuoka Buzen Station, 1968
Family Sepiolidae	
**Euprymna berryi*	Choe, 1966a,b
**Sepiola rondeleti*	
**Sepiola robusta*	
**Sepiola affinis*	
**Sepiola ligulata*	Boletzky *et al.*, 1971; Boletzky, 1974a and 1975c
**Sepietta neglecta*	
**Sepietta obscura*	
**Sepietta oweniana*	Summers & Bergström, 1981
**Rossia macrosoma*	Boletzky and Boletzky, 1973
**Rossia pacifica*	Brocco, 1970
Family Idiosepiidae	
Idiosepius pygmaeus paradoxus	Natsukari, 1970
Order Teuthoidea (squids)	
(Suborder Myopsida)	
Family Loliginidae	
Sepioteuthis sepioidea	Arnold, 1965; LaRoe, 1970 and 1971
Sepioteuthis lessoniana	Choe, 1966a,b; Choe & Oshima, 1963; Inoha & Sezoko 1967; Matsumoto, 1975; Saso, 1979
Loligo vulgaris	Bidder, 1950; Boletzky, 1971, 1974a and 1979b; Neill, 1971; Neill & Cullen, 1974; Tardent, 1962
Loligo pealei	Arnold, 1962; Drew, 1911; Summers & McMahon, 1970 and 1974; Summers *et al.*, 1974
Loligo opalescens	Fields, 1965; Hurley, 1978
Loligo plei (= *Doryteuthis plei*)	LaRoe, 1970 and 1971; Roper, 1965
Doryteuthis bleekeri	Soichi, 1976
(Suborder Oegopsida)	
Family Ommastrephidae	
Illex illecebrosus	Amaratunga *et al.*, 1979; Boucher-Rodoni, 1975; Bradbury & Aldrich, 1969; O'Dor *et al.*, 1977, 1980; Rowe & Mangold, 1975
Todarodes pacificus	Flores *et al.*, 1976 and 1977; Mikulich & Kozak, 1971; Soichi, 1976
Family Enoploteuthidae	Young & Roper, 1977
Order Octopoda (octopuses)	
(Suborder Incirrata)	
Family Argonautidae	
Argonauta argo	Boletzky, in press c, Lacaze-Duthiers, 1892; Naef, 1923; Young, 1960; Zeiller & Compton, 1970
Family Octopodidae	
**Octopus joubini*	Boletzky & Boletzky, 1969; Opresko & Thomas, 1975; Thomas & Opresko, 1973
**Octopus briareus*	Borer, 1971; Hanlon, 1975 and 1977; Messenger, 1963; Wolterding, 1971
**Octopus maya*	Van Heukelem, 1976 and 1977; Walker *et al.*, 1970
Octopus cyanea	Van Heukelem, 1973 and 1976; Wells & Wells, 1970
Octopus defilippi	Grimpe, 1928

Octopus vulgaris	Altman & Nixon, 1970; Itami *et al.*, 1963; Mangold & Boletzky, 1973; Nixon, 1966
Octopus bimaculatus	Ambrose, 1981
Octopus macropus	Voss & Phillips, 1957
Octopus salutii	Mangold-Wirz *et al.*, 1976
Octopus tetricus	Joll, 1976 and 1977
Octopus dofleini	Gabe, 1975; Hartwick *et al.*, 1981; Marliave, 1981
**Hapalochlaena maculosa*	Tranter & Augustine, 1973
Pteroctopus tetracirrhus	Boletzky, 1976, 1981
Eledone cirrhosa	Mangold & Boucher-Rodoni, 1973
**Eledone moschata*	Boletzky, 1975b
**Bathypolypus arcticus*	Macalaster, 1976

TABLE 2

Closed Seawater System Rearing or Maintenance of Cephalopods. This is a partial literature review with representative citations for each species listed in alphabetical order. Asterisk indicates species with benthic young.

Subclass NAUTILOIDEA (nautilus)	
Nautilus macromphalus	Hamada *et al.*, 1980; Mikami *et al.*, 1980
Subclass COLEOIDEA	
Order Sepioidea (cuttlefishes)	
Family Sepiidae	
**Sepiella inermis*	Tang & Khoo, 1974
**Sepia officinialis*	Schröder, 1966; Overath, 1975; Zahn, 1979
Family Sepiolidae	
**Euprymna scolopes*	Arnold *et al.*, 1972
Order Teuthoidea (squids)	
(Suborder Myopsida)	
Family Loliginidae	
Loligo pealei	Brinley and Mullins, 1964; Hanlon *et al.*, 1978 and in prep.; Hulet *et al.*, 1979; Yang *et al.*, 1980a
Loligo opalescens	Hanlon *et al.*, 1979; Hurley, 1976; Yang *et al.*, 1980b, 1983; Hixon *et al.*, in prep.
Loligo plei (= *Doryteuthis plei*)	Hanlon, 1978; Hanlon *et al.*, 1978 and in prep.; Hulet *et al.*, 1979
Doryteuthis bleekeri	Matsumoto, 1976; Matsumoto & Shimada, 1980
Lolliguncula brevis	Hanlon *et al.*, 1978 and in prep.; Hulet *et al.*, 1979 and 1980
(Suborder Oegopsida)	
Family Ommastrephidae	
Ommastrephes sloani pacificus (= *Todarodes pacificus*)	Hamabe, 1963
Order Octopoda (octopuses)	
(Suborder Incirrata)	
Family Octopodidae	
**Octopus joubini*	Bradley, 1974; Forsythe, 1981; Forsythe & Hanlon, 1980 and 1981; Mather, 1972
**Octopus briareus*	Hanlon, 1975 and 1977
**Octopus maya*	Solis, 1967
**Octopus australis*	Tait, 1980
Octopus vulgaris	Itami *et al.*, 1963; Hirayama, 1966; Taki, 1941; Vevers, 1962
Octopus defilippi	Hanlon *et al.*, 1980
Octopus macropus	Taki, 1941
Octopus ocellatus	Taki, 1941; Yamauchi & Takeda, 1964
Octopus burryi	Hanlon & Hixon, 1980
Octopus rubescens	Warren *et al.*, 1974
Hapalochlaena lunulata	Overath & Boletzky, 1974
Eledone cirrhosa	Boyle & Knobloch, 1982

(Overath, 1979), or trickling filters are commonly used to provide filtration in aquaculture systems (see Antonie, 1976; Hirayama, 1974; Spotte, 1979; Wheaton, 1977). Spotte (1979) defines filtration as four processes: biological and mechanical filtration, physical adsorption, and ultraviolet light disinfection. In most open systems only mechanical filtration is used in the form of a settling tank or a sand, gravel or polyester cartridge filter to remove particulate matter and nektonic organisms from incoming water. All four filtration processes are important in closed systems. Biological filtration is accomplished by nitrifying bacteria living in the sand, gravel or biodisc substrates; these bacteria oxidize toxic ammonia to nitrite and then to less toxic nitrate. Mechanical filtration occurs in the sand or gravel filter or in auxiliary filters containing polyester filter fiber and activated carbon. Physical adsorption is accomplished with the activated carbon and with foam fractionators ('protein skimmers', Spotte, 1979); they remove dissolved organics and surface-active organics, respectively. Biological conditioning (when the system is first built) and maintenance are the keys to successful closed systems, and care always must be taken to not exceed the biological carrying capacity of the system. All tank systems should be made of inert materials so that no metal comes in contact with water.

Tank size depends upon the species, but we can make two generalizations: benthic cephalopods can be kept in small tanks, and nektonic, actively swimming cephalopods require large tanks. Benthic cephalopods include most of the sepioids and all the octopodids (cf. Tables 1 and 2) and most of these can be kept in an assortment of tank configurations and sizes. Generally it is advisable to keep small animals in rather small tanks or small compartments screened off from the rest of a large tank. This allows the researcher to keep track of small individuals, to control cannibalism from larger individuals, and to provide sufficiently high food density. Of course excessive crowding must be avoided. According to the animals' habits, the bottom of the tank may be covered with sand or gravel. Many benthic cephalopods (sepioids in particular) take cover in the sand during daytime. Among the nektonic squids, some, like the loliginid squid *Sepioteuthis sepioidea*, orient to the bottom substrates (LaRoe, 1971). For young benthic octopodids, shelters should be available to allow individuals to separate from one another. All tanks must be covered with tightly fitting lids or screens, especially when they hold octopuses or have a high water level. Squids and cuttlefishes do not crawl out of their tanks like octopuses do, but they may jet 'overboard' when frightened.

Larger round tanks are best suited for pelagic cephalopods (e.g., teuthoid squids and micronektonic young of teuthoids and some octopods) because the absence of corners avoids dead spots in water circulation and eliminates the possibility of animals crowding into corners. Also, it is desirable with pelagic organisms that both the cephalopods and their food organisms be distributed as evenly as possible, especially during the very young stages. Evenly distributed illumination from overhead and gentle, uniform flow of water help achieve this (cf. Blaxter, 1968).

C. HATCHING CONDITIONS

Eggs must be handled carefully during collection, and in particular temperature must be maintained within the limits of temperature adaptation of the species involved. This range of adaptation differs among species. The only general rule that can be given is that the eggs of most species can live and develop normally at temperatures around 15 to 18°C. for cold-water species this corresponds to the upper limit of their adaptative range, while for warm-water species it represents the lower limit. Even within the range of natural temperature adaptation, a quick rise of the temperature can be harmful for the embryo, especially at early developmental stages (Marthy, 1972).

Physical parameters measured at the site of capture of juvenile or adult cephalopods do not necessarily fall within the tolerance range of embryonic development. Thus low salinities may be tolerable to adults, but will kill their developing embryos.

If sufficient numbers of newly-laid eggs are available, parallel developmental series kept at different temperatures will provide the neces-

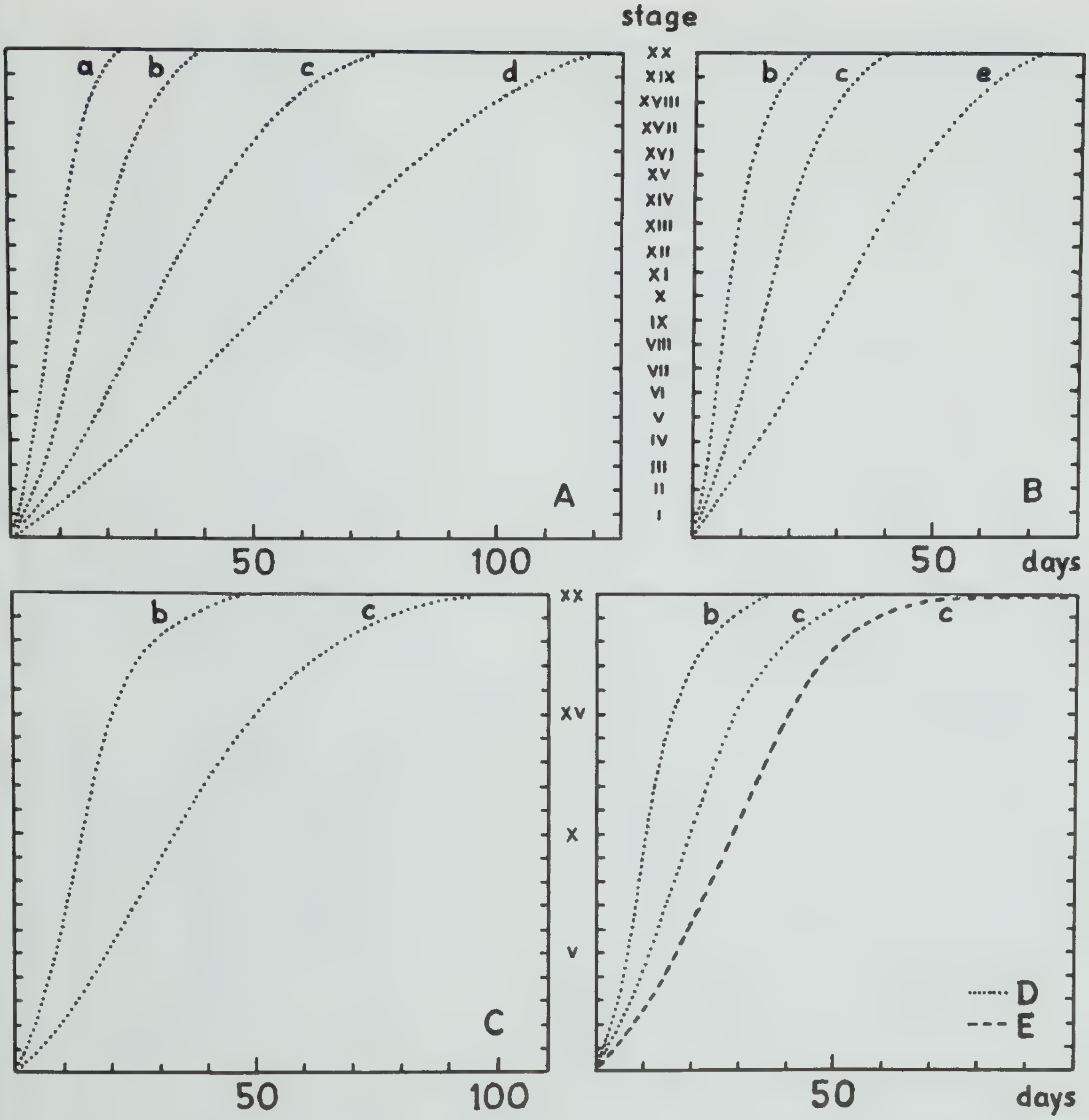

Figure 1. Rates of embryonic development (maxima) at different temperatures in *Octopus vulgaris* (A), *Loligo vulgaris* (B), *Sepia officinalis* (C), *Sepiola robusta* (D), *Rossia macrosoma* (E). a = 25°C, b = 20°C, c = 15°C, d = 13°C, e = 10°C. Stages according to NAEF (1923). (From Boletzky, 1974a).

sary information on temperature adaptation. Concurrently, developmental plots may be drawn by recording at regular intervals the embryonic stages reached at the different temperatures; this allows one to program hatching in later experiments, simply by speeding or slowing embryonic development with higher or lower temperatures (without sudden changes!).

Figure 1 is an example of stage/time plots for the embryonic development of different species. Hatching never can be programmed very precisely. A normal variation of several days must be expected for the total time of develop-

ment. Hatching can be triggered artificially by various stimuli, but this is not advisable unless one can be certain that the embryos are fully developed; in particular the outer yolk sac must have reached a very small size and contain little or no yolk (Figure 2). Premature hatching always increases the chances of early mortality. Embryos become increasingly excitable towards the end of embryonic development, but they are maintained at a low activity level by the effect of a tranquillizing compound contained in the perivitellinic fluid (Marthy *et al.*, 1976). Mechanical stimulation (shaking of the eggs) or a sudden rise in temperature are sufficient to lower the excitability threshold of the animals and to trigger premature hatching.

Optimum conditions for embryonic development in the aquarium are not necessarily ideal for the postembryonic stage. If these conditions differ, one must bridge the gap between the egg-raising system and the rearing system for hatchlings. This is only a minor problem with the eggs and hatchlings of cuttlefishes and sepiolids because the newly-hatched animals settle on the bottom of the tank where they can be manipulated easily.

Screening of the outflow pipe is important with the actively swimming hatchlings of squids. Air bubbles should not be used in a tank holding squid hatchlings, because the small animals are easily caught in the stream of bubbles and air bubbles often adhere to their skin. Air stones must be placed in a compartment walled off from the main tank. In all instances, screens, especially those placed around the outflow, must allow slow water flow at all times. The mesh size must be small enough to prevent animals (including food organisms) from passing through the screen, yet large enough to allow the water to flow freely. The total surface area of the screen should be large. Uneven mesh distribution should be avoided, as the water flow through larger openings may be higher than the hatchlings can counteract by jetting. All screens should be cleaned frequently, because micro-fouling alters the flow characteristics. Clogging of mesh results in a rise of water level, which in turn raises the flow speed in the upper 'clean' part of the screen.

One of the safest methods to ensure normal

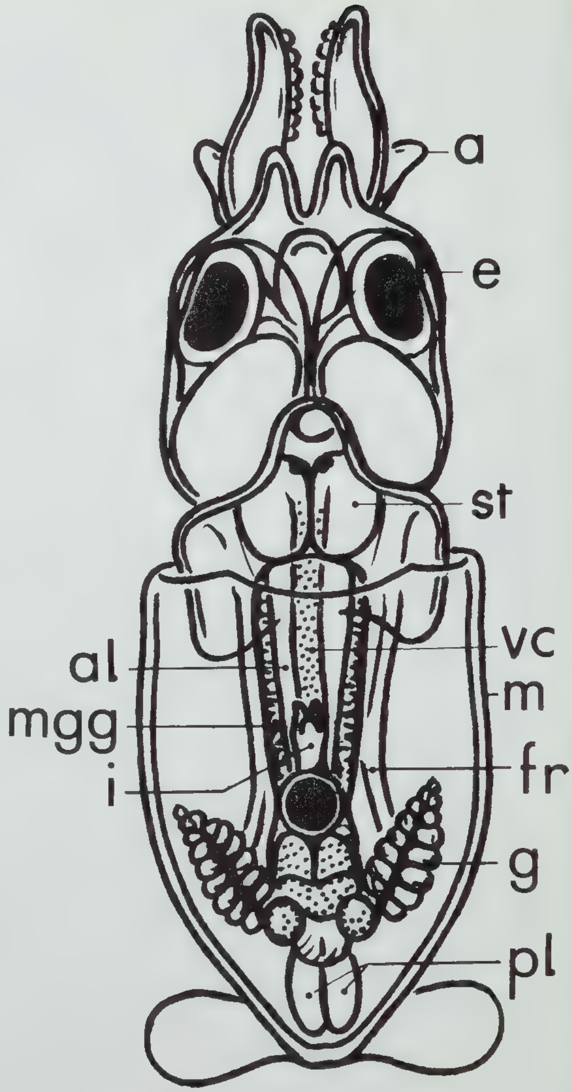

Figure 2. Semi-schematic presentation of a newly-hatched *Loligo vulgaris* in ventral view. The outer yolk sac amidst the arms has disappeared, whereas the inner yolk sac is still sizable. Its anterior lobe (a) lies between the two large lobes of the midgut gland (mgg). The posterior lobes (pl) of the inner yolk sac reach to the posterior end of the visceral complex. Other organs are the intestine (i), the gills (g), the funnel retractors (fr), and the vena cephalica (vc), all lying within the mantle (m). Dorsally to the funnel lie the statocysts (st). In front of the large optic lobes and on either side of the buccal mass lie the eyes (e). The arm crown comprises the two long tentacles and the shorter arms (a). (From Boletzky, 1975a.)

hatching for squids, in addition to optimal rearing conditions, is to suspend egg capsules singly in the rearing tank. Egg clusters should not be suspended as a whole, because the gentle water flow (ensure the absence of air bubbles!) may be insufficient to ensure oxygenation of the inner parts of the egg mass. Furthermore, separately suspended egg capsules allow optimum conditions for hatching, because the animals emerge into open water as soon as they penetrate the surface of the gelatinous envelopes. The process of penetrating these envelopes is 'fully automatic', because the integumental ciliature drives the animal through the 'bore hole' made by the hatching gland (Boletzky, 1979c). As squids tend to hatch during nighttime, hatching can be delayed to some extent by constant lighting of the tank. High light levels have caused excessive algal growth on egg clusters of *Loligo opalescens* (Yang, pers. comm., 1982); therefore it is advisable to maintain lighting at low intensity.

Most octopuses 'brood' their eggs and this necessitates slightly different techniques. If the mother octopus does care for the eggs, the bulk of the egg mass by all means should be left with the animal to ensure the natural oxygenation and cleaning functions. The swimming hatchlings can be collected by channelling the water from the (unscreened) overflow of the brooding tank into a large holding tank placed next to it. The overflow of the latter must be screened. This method also can be used for species having bottom-living hatchlings, but the young animals settled in the brooding tank should be collected regularly. Samples should be taken from the egg mass long before hatching, to closely follow embryonic development. Development can be speeded up by increasing temperature so that preliminary rearing trials can be run before the bulk of hatchlings arrives. Normal hatching continues over several days or weeks, according to the length of time during which the eggs have been laid.

All octopus eggs taken from the egg mass are endangered by fouling, because the unprotected chorion very quickly becomes colonized by microorganisms. To prevent this, the eggs should be kept in very clean sea water. An effective method to keep small-sized eggs is to spread them out in small numbers in Petri dishes in a few millimetres of filtered sea water, which must be changed daily. The low water level permits rapid oxygen diffusion. Large octopus eggs do not always develop under these conditions, probably because the large yolk mass settles in the chorion, which may impede the epibolic growth of the early blastodisc. These eggs should therefore be kept floating, e.g. in a funnel (of inert material) with a gentle water jet or stream of air bubbles rising from the funnel tube. The hatching mechanism of octopuses functions independently of the egg-care of the mother animal (Boletzky, 1966).

Although newly-hatched animals start to feed actively only hours or days after hatching, they always do so before their yolk reserves in the internal yolk sac are completely consumed (Boletzky, 1975a). Living prey organisms therefore should be present as early as possible. Prey organisms should be of a size no larger than the size of the hatchling. Indeed, this size relationship should be adhered to throughout rearing.

Adverse effects of confinement in rather small tanks can be alleviated for actively swimming animals, especially squids, by allowing them to locate visually the boundaries of their artificial environment at all times. Total darkness at night must be avoided; a dim source of artificial light is sufficient for their vision. However, sudden exposure to bright lights without a transition time after the period of dim light must be avoided, since it often produces a 'panic' reaction that can result in the animals injuring themselves.

The correct choice of tank systems and of food organisms is essential for the success of a rearing project. It is stressed here that the hatchlings must be placed as early as possible in the artificial environment in which they must live in subsequent months. The substrate chosen for the bottom of the rearing tank must satisfy the behavioural patterns of the animal as well as the experimental requirements, especially the necessity of keeping track of the reared animals and of the food organisms.

The change from the protected micro-environment of the egg-case to the open water exposes the animal to many dangers even in the

absence of predators. Very close observation of early rearing conditions by the experimentor is essential in limiting hazards.

D. DISEASES, PARASITES AND PREVENTION

Very little is known about diseases in cephalopods (Hochberg, this volume). Presently there are only few reported cases of diseases or parasites which have seriously affected the maintenance of cephalopods (cf. Polglase, 1980).

In squids, fin damage from abrasion (Boletzky, 1974c) and subsequent bacterial, fungus or protozoan infections (Leibowitz *et al.*, 1977; Hulet *et al.*, 1979; Hochberg, pers. comm.) cause difficulty in carrying out forward attack movements on prey, so that starvation and infection soon lead to death. Prevention of fin damage is the only known remedial action (see also Marthy, 1974a,b).

In octopuses, Forsythe and Hanlon (unpublished data) have noted significant mortality from bacterial infections of the mantle skin during a large-scale pilot culture of *Octopus joubini* in closed systems. Nifurpirinol and tetracycline treatments in separate aquaria showed signs of alleviating the condition; Poupard (1978) stated that these antibacterial agents may have little adverse effect on beneficial nitrifying bacteria in filter beds, and therefore they hold promise for future treatment of skin damage. Yang *et al.* (1980b; in press) quarantine and, in some instances, prophylactically treat food organisms fed to reared squids with antibacterial agents such as chloramphenicol, erythromycin and tetracycline; they also treat crustacean food organisms such as mysidacean and palaemonid shrimp with quinicrine to eliminate protozoan ectoparasites. Future work should evaluate the effectiveness of antiparasitic agents such as quinacrine, which is used by Yang *et al.* (1980b) to treat food organisms fed to reared squids.

In laboratory culture, attention must be focused on bacterial and viral infections, especially those precipitated by overcrowding. Little is known about viruses in either squids (Devauchelle & Vago, 1971) or octopuses (Rungger *et al.*, 1971). Fungi have been reported to cause fatal lesions in the octopus *Eledone cirrhosa* (Polglase, 1980). There are numerous reports of parasitic infestations in wild-caught cephalopods (see reviews; Dollfus, 1958; and Hochberg, this volume). Hochberg (this volume) reviews the parasites of cephalopods and discusses potential parasite problems in culture.

Ultraviolet light or ozone often are used for disinfection of culture water, but their application and effectiveness in different culture designs are controversial. Spotte (1979) provided a recent synopsis of both methods. A great deal more directed research on their usefulness in controlling pathogens in marine systems must be done before they can be recommended for cephalopod culture.

Diets of Cephalopods

A. THE NATURAL DIETS OF CEPHALOPODS

The dominant prey organisms of cephalopods are crustaceans, other molluscs and fishes. Actively moving prey are located visually in most species, pursued and—if they are unable to escape—seized with the tentacles or arms. The relative size of the prey may be very large, sometimes similar to the size of the cephalopod predator. Large prey generally is reduced to pieces by the strong beaks; these pieces are grasped by the radula and swallowed. It has been observed also that very large prey sometimes may be swallowed whole (Bidder, 1950; see also Bidder, 1966 for records of food by various authors, and Boucaud-Camou and Boucher-Rodoni, 1982).

The stomach contents of a cephalopod may yield very precise information on the animal's natural diet, but often the stomach of freshly caught animals either is empty or contains material that is not easily identified. In samples obtained by trawling or dredging, the animals taken together with cephalopods may be considered potential prey, but unless they are recognized in the stomach contents of the cephalopods one cannot be certain. Also, it cannot be excluded that some abnormal predation occurs in a trawl net during the course of a tow.

In bottom dwelling octopodids, the exoskeletons and shells of crustaceans and molluscs often are found as 'middens' that

allow identification of the food animals, provided it can be established that the remains were actually eaten by the octopus. Analysis, however, may be misleading because smaller crustacean parts often are washed away by currents.

Direct observations of cephalopod predation in the sea, generally by divers, largely are restricted to a few species of cuttlefishes, loliginid squids, and octopuses (cf. Lane, 1960; Altman, 1967; Hochberg & Couch, 1971; Hanlon, 1975; Hanlon & Hixon, 1980).

B. DIETS FOR CEPHALOPODS IN EXPERIMENTAL WORK

Many bottom-living cephalopods, in which energy consumption for locomotory activity may be very low, can survive for days or even weeks without food. For certain experimental purposes, this tolerance to starvation is most helpful, but for long-term maintenance a minimum supply of food is necessary.

According to Grimpe (1928) cephalopods that survive in the aquarium feed almost exclusively on crustaceans, and all of them show clear preference for living prey. Grimpe (1928) summarized knowledge of the diets of cephalopods up until that time, but recent work has shown that cephalopod diets are more diverse. The following sections update his summary.

The problems of food density in cephalopod culture also have been approached by Grimpe (1928) who stressed the 'voraciousness' of most cephalopods, but he made it clear that precise figures on optimal food intake were not available. Borer (1971) found that food intake in *Octopus briareus* and *O. bimaculoides* increased in proportion to the number of prey (crabs) offered daily and decreased following a reduction in prey size. In contrast, food density is much more difficult to define with nektonic cephalopods that have to be given greater tank space; these problems have been discussed by Yang *et al.* (1980a,b; 1982; see also Hirtle *et al.*, 1981).

1. Subclass **NAUTILOIDEA**
   i. Order NAUTILOIDEA
      a. Family NAUTILIDAE

Nautilus spp.

Willey (1902) summarized his experience with the feeding habits of the Pearly Nautilus. He stated that stomach contents indicated a crustacean diet under natural conditions, and added that 'any kind of animal bait will tempt *Nautilus*, and after a full meal the crop is found to be gorged to repletion'.

Bidder (1962) described the feeding of *Nautilus macromphalus* and *N. pompilius* in aquaria. In these observations of animals that survived for up to 8 weeks in captivity, pieces of fishes or crabs were fed to the animals.

Cousteau (1971) reported on a *Nautilus* from New Caledonia that lived for two months in the Monaco Aquarium, feeding on sardines. More recently, *N. macromphalus* has been regularly on display in Monaco (see also Packard *et al.*, 1980, Hamada *et al.*, 1980, and Ward, in press).

Haven (1972) maintained *Nautilus pompilius* in holding cages set at different depths in the sea and in aquaria. The animals were fed live and dead crabs and fishes, and pieces of chicken. At least part of the natural diet of *Nautilus pompilius* was found to consist of small crabs (ca. 1 cm carapace width). Haven suggested that this species is a bottom feeder and that possibly in addition to feeding on small crustaceans, it is a scavenger.

Ward and Wicksten (1980) analysed the stomach contents of *Nautilus macromphalus* in New Caledonia and found hermit crabs (*Aniculus aniculus*) to be the most important prey, followed by small brachyuran crabs. Fish and lobster (*Panulirus*) fragments also were found, and on several occasions *N. macromphalus* was observed in the natural habitat ingesting portions of newly molted lobster exuviae (*P. longipes*).

Mikami *et al.* (1980) used pieces of jack mackerel (*Trachurus japonicus*) and shrimp (*Pandalus borealis*) as food for *N. macromphalus* in the Yomiuri-Land Marine Aquarium (Tokyo). They also noted that the animals could not capture live fish (*Abudefduf assimilis*), crabs (*Hemigrapsus sanguineus*) or annelids, which are all fast-moving prey.

Carlson (1977) stated in 'The Chambered Nautilus Newsletter' that *N. pompilius* shipped from Fiji to the Waikiki Aquarium (University

of Hawaii) were 'fed one fresh shrimp or chunk of fresh tuna every other day (occasionally every day), but they will not eat twice a day'.

2. Subclass **COLEOIDEA**

i. Order SEPIOIDEA

The Sepioidea or cuttlefishes are one of the two groups of decapodous cephalopods. The sepioids generally live at moderate depths and in close relation to the sea bottom. There are only two pelagic forms among them: *Spirula* with its coiled chambered shell, and the sepiolid *Heteroteuthis*. All the others spend most of their time on the sea bottom, and many hide in sandy and muddy substrates during day-light hours and thus remain quiescent for long periods.

Whereas *Spirula* and *Heteroteuthis* never have been kept in aquaria for more than a few days, some of the common benthic or nekto-benthic species of *Sepia* and of several sepiolids have been reared from hatching to the adult stage.

a. Family SEPIIDAE

Sepia officinalis

Najai and Ktari (1974) analysed the stomach contents of more than 500 individuals of *S. officinalis* from the Tunisian coast. They identified the following food items: crustaceans (*Penaeus* sp. and other decapods; *Sphaeroma*, *Cymodocea* and other isopods; copepods; and ostracods), bony fishes, molluscs (octopod and decapod cephalopods, lamellibranchs, gastropods, and pteropods); a few worms (polychaetes and nemerteans); and algae (in two stomachs).

In a study of the feeding behaviour of newly hatched *S. officinalis*, Wells (1958) showed that young animals of this species regularly attack and eat mysids (*Mysis* sp.). These observations have been confirmed by others. In addition to mysids (*Praunus* sp.), very young cuttlefish can be fed on small prawns (*Leander* spp., *Crangon* spp.) and on amphipods (*Gammarus* spp.), as reported by Schröder (1966). This author cultured *S. officinalis* through two consecutive generations in the Berlin Aquarium, where the half-grown and adult animals fed on fishes and crabs (*Carcinus* sp.).

Messenger (1968) analysed the visual attack of *Sepia*, on prawns and crabs in particular. Additional observations are reported on young cuttlefishes feeding on fish fry (*Mugil* sp.), and on adults eating mantid shrimps (*Squilla* sp.) and smaller *Sepia*.

Neill and Cullen (1974) used young mullet (*Mugil* spp.) in experiments on the hunting behaviour of cuttlefishes. They found that attacks were more successful with single prey animals than with schooling prey, and they described the sequence of actions during an attack. Their observations complement those of Messenger (1968).

Richard (1966, 1975) cultured *S. officinalis* for experimental purposes in a marine laboratory. His observations indicated that very young animals accepted amphipods (*Marinogammarus marinus*, *M. stoerensis*, *Gammarus zaddachi*) and that optimum growth in juvenile and adult animals was obtained with a varied diet including prawns (*Crangon vulgaris*, *Palaemonetes varians*, *Palaemon serratus*), crabs (*Carcinus maenas*, *macropipus holsatus*) and fishes (*Gobius minutus*, *Cottus bubalis*, *Pholis gunellus*, sole, herring). Richard (1971) also suggested that newly hatched *Sepia* might be fed brine shrimp (*Artemia*) which can be obtained easily by mass culture. However, the growth rates obtained with these clearly were lower than with natural diets such as mysids and palaemonid or crangonid prawns (Pascual, 1978; Boletzky, 1979b).

Overath (1975) fed *Daphnia* to newly hatched *Sepia* and after two weeks, small *Crangon* sp. and *Astacus leptodactylus*. More recently Féral (1977, 1978) reared *Sepia officinalis* with the following diets; hatchlings with mysids (*Paramysis nouveli*, *Praunus flexosus*) and adult *Artemia salina* until they attained a length of about 5 cm. Larger cuttlefishes, 5 to 10 cm long, were fed crustaceans (*Crangon crangon*, *palaemon serratus*, *Orchestia marina* and young *Carcinus maenas*) and fishes (*Pomatochistus microps*, young *Mugil auratus* and *Onus mustellus*). For still larger animals, the prey offered were crabs (*Carcinus maenas*), large prawns (*Palaemon serratus*) and various species

of fishes (*Gobius paganellus*, *Blennius* sp., *Ammodytes lanceolatus*, *Onos mustellus*, *Mugil auratus*).

Yim (1978, see also Yim & Boucaud-Camou, 1980) used natural zooplankton to feed very young cuttlefish, up to ten days old, and *Mysis* or very small *Crangon crangon* thereafter.

Pascual (1978) cultured *Sepia officinalis* through three generations feeding young animals on various diets composed of *Diamysis bahirensis*, *Mesodopsis slabberi*, *Palaemonetes varians*, and *Artemia salina*. Larger animals were given *Palaemonetes*, *Carcinus maenas*, *Engraulis encrasicholus*, *Atherina presbiter*, *Sardina pilchardus* and *Mugil auratus*.

Unless they are underfed or actually starving, cuttlefishes generally take live prey only, or else dead prey that is artificially kept in motion. Such prey may elicit attack and seizure by the cuttlefish even above the water surface (Boletzky, 1972). The upper size limit of a type of prey that will be attacked by a cuttlefish varies among individuals, and also it may depend on the momentary motivation for feeding. As a general rule, the total length of a fish or prawn should not be greater than the total length of the cuttlefish; the carapace width of a crab should correspond to not more than one half of the dorsal mantle length of the cuttlefish (cf. Boletzky, 1974a). There is no definite lower size limit for prey. Very hungry *Sepia* will attack very small prey, small mysids for example, which usually they are unable to seize with their tentacles when half-grown or adult.

Underfed *S. officinalis* may survive for many months (Boletzky, 1974b, 1979b), and with a regular minimum supply of food their growth rate can be kept extremely low (ca. $\frac{1}{10}$ of normal linear growth) from hatching to an age of one year or more. The minimum food requirements can be recognized from the buoyancy of the animals; starving animals generally float at the surface and are unable to remain on the bottom if they have been successful in descending by jet propulsion. After feeding they soon attain neutral buoyancy (cf., Denton & Gilpin-Brown, 1973). To facilitate their attack on moving prey, one may place starved cuttlefish in a tank with a very low water level, so that they float just above the bottom, or the prey may be presented at the water surface (e.g., suspended on a thread).

Among the earliest signs of starvation is the appearance of a longitudinal dark stripe on the dorsal side of the mantle, caused by the concentration of chromatophores resulting from skin contraction. The life cycle is summarized by Boletzky (in press, a).

Sepia lycidas

In a report of the Fukuoka Buzen Fisheries Experimental Station (1968), young animals within 12 hours of hatching attacked and ate various shrimps 5-12 mm long (*Metapenaeus joyneri*, *Palaemon pacificus*, *Crangon* sp., *Leander* sp.). Frozen food also was accepted (shrimps, fishes, clams, pelletized food), but only live shrimps, especially *Crangon* sp., yielded good results, with an average daily food ingestion of 0.1 g per individual in the first weeks after hatching. Larger juveniles were transferred to pond cages and fed larger *Crangon* sp., *Palaemon* sp., and later gobies and sliced fish.

Sepia latimanus

Inoha (1971) reported that eggs were laid in corals of the genus *Millepora*. The hatchlings had a dorsal mantle length about twice as large (13.5-15.8 mm) as in *Sepia officinalis*. They attacked and ate *Palaemon* sp. and other shrimps, whereas fast moving fish larvae (mullet, *Apogon lineatus*, *Chromis notata*) were able to escape.

Sepia esculenta, *S. subaculeata*, *Sepiella maindroni*

Oshima and Choe (1961), Choe and Oshima (1963), and Choe (1966b) reared these species of cuttlefishes in the laboratory from hatching to an age of four months. They used living *Neomysis japonica* as food for the young animals. In the older ones, the living prey were replaced by 'minced fish meat or salted mysis-shrimp placed on the bottom of the tank'. Choe (1966b) noted a lower growth rate in animals fed on dead food as compared to those fed on live prey. In a short-term experiment on the feeding rates of the three species of cuttlefishes, Choe also used *Leander serrifer*.

Eugusa (pers. comm.) wrote that 'a large-scale experiment on the culture of *Sepia*

subaculeata was done with considerable success by the Fukuoka Prefectural Fisheries Experimental Station.' The young cuttlefishes started to feed 12 hours after hatching, living shrimp larvae 5-12 mm long being the best food; frozen larvae were seized in mid-water (not on the bottom!). However, for cuttlefishes ten days old, live prey could be replaced (entirely) by frozen shrimp, and 20 days after hatching, the young *Sepia* accepted fish meat.

Sepiella inermis

Tang and Khoo (1974) studied prey selection (type and size of prey) in this small species of cuttlefish. Prey organisms used in their experiments were fish (*Poecilia reticulata*), prawns (*Acetes* sp.), and crabs (*Dotilla* sp.); they 'corresponded quite closely to the type and size of prey consumed by *Sepiella inermis* in the natural environment'.

b. Family SEPIOLIDAE

Rossia macrosoma

This fairly large species of the sepiolid subfamily Rossiinae has been reared in the laboratory by Boletzky and Boletzky (1973) from hatching to the age of eight months. The animals were fed live prawns (*Leander serratus*) from hatching onward. The maximum length of the prawns presented was roughly twice the mantle length of *Rossia*. Mysids were rarely captured by the young animals. Crabs, even very small individuals, never were taken.

Rossia pacifica

This species rests in shallow depressions in shrimp beds and 80% of its diet consists of shrimps, although crabs, mysids, small fishes and cephalopods also are eaten (Brocco, 1970; Hochberg & Fields, 1980).

Euprymna berryi

Choe and Oshima (1963) and Choe (1966b) briefly reported on the laboratory rearing of this small species of subfamily Sepiolinae. The hatchlings were reared to the age of about two months with live mysids.

Euprymna scolopes

Arnold *et al.* (1972) used adult *Leander debilis* as food for adult animals of this species. Occasionally small *Gambusia affinis* were offered. Young animals hatched in the laboratory were fed on larval and adult *Anisomysis* sp., adult *Artemia salina*, and occasionally on newly-hatched *Octopus cyanea*. They were reared to the age of nearly seven months. The life cycle is reviewed by Singley (in press).

Sepiola spp. and *Sepietta* spp.

Boletzky *et al.* (1971) reared four species of *Sepiola* (*S. rondeleti*, *S. robusta*, *S. affinis*, *S. ligulata*) and two species of *Sepietta* (*S. obscura*, *S. neglecta*) from hatching to the adult stage (see also Boletzky, 1974a, 1975c). All the young animals were fed on mysids (*Leptomysis mediterranea*); older juveniles and adults were fed small *Leander* spp. In the area of Banyuls-sur-Mer (western Mediterranean) *Sepiola robusta* is caught regularly at depths of a few metres on a sandy bottom (in which it hides during daylight hours), together with the crangonid prawn *Philocheras* spp. (Boletzky, in press, b). A recent series of experiments has shown that sepiolids as well as young *Sepia officinalis* can be fed exclusively *Philocheras* if this prey is available in sufficient numbers (personal observations).

Summers and Bergström (1981, and pers. comm.) cultured *Sepietta oweniana* to the second generation in open seawater systems in Sweden. The large benthic hatchlings (5 mm ML) fed 'mixed, shallow-benthic arthropods which were sorted only by straining out those things which would not pass a 2 mm sieve'. they would not eat brine shrimp or fishes. At three months, they showed a preference for the mysids *Praunus flexuosus* and *P. inermis*, but also would accept the shrimps *Palaemon elegans*, *Thoralus cranchi* and *Crangon crangon*. Growth on this diet averaged 4 mm per month to maturity. Stomach contents of 515 wild-caught specimens showed that 7.2% had food in the stomach and that 80% of the remains were shrimps and euphausiids. Bergström and Summers (in press) reviewed the life cycle of *S. oweniana*.

ii. Order **TEUTHOIDEA**

The majority of the squids, which form the largest taxonomic group of the recent cephalopods (in terms of the number of families and genera), are pelagic animals that

live in coastal and offshore waters. Among the oegopsid squids only two ommastrephids that live at least part of the year in rather shallow water have been used for long-term laboratory investigations. The only squid species that have been reared from hatching in the laboratory so far belong to the Loliginidae, which generally live close to shore. However, these animals are nektonic, as are all squids, and although they live close to the bottom, apparently they do not remain quiescent even for short periods under natural conditions. The high energy requirement of this continually active mode of life necessitates a high food intake in growing squids, with daily rates at least around 50% and occasionally higher than 100% of the predator's own weight (cf. LaRoe, 1971).

a. Family LOLIGINIDAE

Sepioteuthis lessoniana

Choe and Oshima (1963) reared this species from hatching to the age of 45 days on a diet of live mysids (*Neomysis japonica*), obtaining a daily increase of the squid's body weight between 7 and nearly 11% (Choe, 1966b).

Inoha and Sezoko (1967) fed larvae of *Macrobrachium* to young *Sepioteuthis*. Saso (1979) reared this species to the age of 170 days on a diet of fish larvae (*Atherina bleekeri*), small anchovies (*Engraulis* sp.), and later on larger *Atherina bleekeri* and *A. japonica*. Matsumoto (1975) fed horse mackerel and anchovy to wild-caught *S. lessoniana* (30-60 g) held in cages in the open sea and obtained a tenfold weight increase in about two months.

Sepioteuthis sepioidea

LaRoe (1970, 1971) reared this species from hatching to sexual maturity at nearly five months of age. The young animals were fed on coral reef mysids (*Mysidium columbiae*, *M. integrum* and *Heteromysis actinea*) and juvenile or larval fishes (*Gambusia* sp., *Poecilia* sp.). A variety of other prey were tried but were not eaten regularly by the young squids (e.g. copepods, including some large *Acartia* sp., chaetognaths, pelagic polychaetes, *Artemia salina*, zoea and megalopa stages of various crabs and other crustacean larvae, amphipods, very young crabs and shrimps).

Larger squids were fed primarily on fishes (anchovies, *Anchoa* sp.; mollies, *Poecilia* spp.; mojarras, *Gerres* sp.) and penaeid or palaemonid shrimps (cf. Arnold, 1965, who used pilchards and other small fishes). LaRoe notes that 'each of the foods found was only suitable for a definite size range. The squids would not attack prey that were too large or too small. Between the 21st and 26th day they ceased to attack mysids; by this time they were about twice as long in total length (ML about 1 to 1½ times longer) as mysids'.

Loligo vulgaris

In contrast to *Sepioteuthis*, the eggs of this species are small, and the hatchlings have a mantle length of about 3 mm, which is about half of that in newly-hatched *Sepioteuthis* (ca. 5 mm in *S. sepioidea*, 6-7 mm in *S. lessoniana*). Consequently the upper size limit of suitable prey is considerably smaller than with young *Sepioteuthis*.

Bidder, in an appendix to the paper by Portmann and Bidder (1928), reported on experiments aimed at the laboratory culture of hatchlings of *Loligo vulgaris*. The only positive indication of prey capture in the newly hatched squid was found with the copepod *Temora longicornis*, whereas captured oyster veligers were dropped 'as if in disgust'.

Boletzky (1971, 1974a, 1979a) fed hatchlings of *L. vulgaris* with young *Leptomysis mediterranea*, the telson and uropods ('tail fan') of which had been cut off in order to slow down the escape movement of this prey. This diet was supplemented by half-grown *Artemia salina* and crustacean larvae.

Larger juveniles and adults captured from the sea were used in an experimental study of the digestive mechanism by Bidder (1950). The experimental animals were fed small dead fish and pieces of fish, which they captured in midwater. Bidder observed that 'once food had fallen on the bottom, it was rarely taken again. Pieces of food suspended on threads in midwater were always ignored. The most successful method was to balance food on a loop of wire, fixed into the end of a long piece of glass tubing, so that neither operator nor tool was visible to the squid, and to let the food fall in as gently as possible'. Bidder also used *L. forbesi*,

Alloteuthis media and *A. subulata*, in this study.

Tardent (1962) reported that young *L. vulgaris* (4-10 cm in mantle length) caught with night lights were kept regularly in the Naples Aquarium for periods up to two months. The squids were fed with pieces of sardines and live shrimps (*Lysmata* sp., *Leander* sp.). In contrast to the observations of Bidder (1950), Tardent found that 'food is as readily picked up from the bottom or walls of the tank as from the water surface', and he concluded that *L. vulgaris* 'seems to have much closer relations to the bottom than one might think'. Neill and Cullen (1974) studied the hunting behaviour of *L. vulgaris* using live fish (*Atherina* sp.) as prey. Worms (in press) reviewed the life cycle.

Loligo opalescens

The earliest attempts to rear the hatchlings of *Loligo opalescens* were made by Fields (1965). The food offered included newly hatched larvae of the copepod *Tigriopus fulvus* and of *Artemia salina*, motile cells of different algae, the diatom *Nitzschia closterium minutissima*, and fine planktonic material. The young squids were not observed to feed, and all died within ten days of hatching.

Hurley (1976) was successful in rearing *L. opalescens* to a maximum age of 100 days on a diet of *Artemia* nauplii and adults. The hatchlings, which are similar in size to those of *L. vulgaris* (mantle length 2.7 mm) readily attacked the nauplii (length 0.7 mm) and small adults of *Artemia salina* (5 mm long), copepods (1 mm long) and larval fishes (4 mm long). In an experiment with squids aged 49 days, a great number of larvae of the chub mackerel, *Scomber japonicus*, were presented to animals that had been feeding on adult *Artemia* of comparable size. The number of the fish larvae presented was about equal to the number of *Artemia* (of similar size) present in the tank. The squid attacked the fish larvae much more frequently than the *Artemia*, but only few attacks on the former were successful. In contrast to what LaRoe (1971) observed in *Sepioteuthis sepioidea*, Hurley found that young *L. opalescens* 'must be considered as predators on a wide range of prey types and prey sizes'. This author also cited a personal communication of McGowan, saying that young *Loligo opalescens* successfully attack the mysid *Metamysidopsis elongata*.

Hanlon *et al.* (1979) reared the hatchlings of *L. opalescens* to a mantle length of 17.3 mm in 79 days principally on a diet of copepods. The hatchlings vigorously attacked the large, slow-moving, white colored copepod *Labidocera aestiva* (3.0 to 3.5 mm long). Three weeks later at a mantle length of 5 to 6 mm the squids also ate the larger blue copepod *Anomalocera ornata* (5.0 to 5.5 mm long). Young squids of 6 to 9 mm ML also readily attacked and ate the clear copepods *Eucalanus hyalinus* (6.0 to 6.5 mm long). *Artemia* nauplii and adults were eaten at times of low copepod availability, but squids that were fed exclusively on brine shrimp (*Artemia*) did not survive beyond ten days. Squids did not feed on barnacle nauplii (*Balanus* spp. 0.2 to 0.5 mm). Squids showed a clear preference for copepods, and the growth rates obtained on this diet were slightly higher than reported by Hurley (1976). Mortality was attributed to fluctuating food availability and, in later stages, to fin damage.

Yang *et al.* (1980b, 1983), based on the results of Hanlon *et al.* (1979), used large-scale closed systems to rear the hatchlings to near sexual maturity at a mantle length of 77 mm after 233 days. The diet consisted of copepods, other crustaceans and fishes. During the first 70 days the squids readily attacked and ate the copepods *Acartia tonsa* (0.8 to 1.2 mm), *Labidocera aestiva* (1.5 to 2.5 mm) and *Anomalocera ornata* (2.0 to 3.0 mm). During the same period, squids were fed *Artemia* nauplii and adults (0.3 to 4.0 mm) as a supplementary food source, and they were seen to attack and eat chaetognaths. From days 60 to 130 the young squids (5 to 25 mm ML) were fed the myses and postlarvae of the pink shrimp *Penaeus duorarum* (2.5 to 6.0 mm) and the mysid shrimp *Mysidopsis almyra* (2 to 10 mm). Beginning at day 100 the growing squids were fed an assortment of shrimps and fishes including the grass shrimp *Palaemonetes pugio* (1.5 to 25 mm) and the estuarine fishes *Fundulus similis* (8 to 35 mm), *Menidia beryllina*, *Adeinia xenica*, *Fundulus grandis*, *Cyprinodon variegatus*, *Gambusia affinis* and *Mugil* spp. (all

15 to 70 mm). Growth on this diet was 1.69 per cent per day and mortality was attributed to starvation and fin damage.

Hixon and his co-workers (in prep.) have cultured *L. opalescens* through to sexual maturation and egg laying. The techniques, foods and tank systems were similar to those described above, except that food was made available constantly and at higher densities. Growth rate was nearly double the previous experiments of Yang (1980b, in press). Egg laying occurred on day 184 in a female approximately 85 mm ML. For the first time the reared squids showed cannibalism, which coincides with observations of natural populations off the coast of California. Adult feeding dynamics of *L. opalescens* have been studied by Karpov and Cailliet (1978).

Hochberg and Fields (1980) noted that adults fed on euphausiids, mysids, fishes, benthic polychaete worms and their own young. Loukashkin (1976) analyzed stomach contents of 1000 adult *L. opalescens* and found that, among the 33% of stomachs with food, 42% had crustacean remains, 20% fish remains and 14% polychaete worms and miscellaneous material. The pelagic red crab *Pleuroncodes planipes* has been observed to be eaten by *L. opalescens* (Siger, pers. comm.). A review of the live cycle of this squid species is given by Hixon (in press).

Loligo pealei

The small hatchlings of this species (1.6 mm ML) are similar in size and morphology to those of *L. plei* (McConathy *et al.*, 1980). Chanley (unpublished report, 1976) fed them egg yolk and minced mussel meat with maximal survival of 13 days. Haefner (1959) indicated from stomach content analyses of *L. pealei* in Chesapeake Bay that young squids prefer a diet of shrimps, and larger squids prefer fishes.

The only success in rearing the hatchlings has been by Yang *et al.* (1980a) who reared one squid to 3.3 mm ML in 40 days. The general methodology and tank design were similar to that in Hanlon *et al.* (1979). They fed on very small copepods (*Acartia tonsa*, *Labidocera aestiva* and others). Very small rotifers (*Brachionus pliciatilis*), marine cladocerans (*Diphanosoma* sp.) and *Artemia* nauplii were not readily taken.

Adult *L. pealei* have been maintained for periods of varying length up to 28 days by Drew (1911), Arnold (1962), Summers and McMahon (1970, 1974), and Summers *et al.* (1974) using the estuarine fish *Fundulus* as food. Hanlon *et al.* (1978 and in prep.) maintained this species up to 71 days on a fish and shrimp diet similar to that described for *L. plei.*

Whitaker (1978) studied the biology of *L. pealei* and *L. plei* on the southeastern coast of the United States. Dominant prey were fishes, followed by crustaceans and squids. A small proportion of stomach contents also contained chaetognaths and some miscellaneous items (see also Vinogradov & Noskov, 1979). Vovk and Khvichiyia (1980) analyzed feeding in juvenile *L. pealei* and found that main food objects were young fishes, copepods, squids, chaetognaths, euphausiids and other shrimps. The change from mesoplanktonic to macroplanktonic food was observed at a size of about 8 cm ML, and to the adult type of feeding between 12 and 16 cm ML. Macy (1982) found that, overall, crustaceans were more frequently consumed than either fishes or squids. However, there was a general trend for squids less than 15 mm ML to consume more crustaceans, while those over 15 mm ML consumed more fishes. Summers (in press) reviewed the life cycle of *L. pealei*.

Loligo plei (= *Doryteuthis plei*)

The small hatchlings of this species are only 1.5 mm ML (Hanlon *et al.*, 1979 Figure 1; McConathy *et al.*, 1980), and they have not been reared yet. Hanlon (1978) tried rearing them in small aquaria on *Artemia* nauplii, rotifers (*Brachionis pliciatus*) and small copepods but none survived beyond three days. In a separate experiment, young wild-caught juveniles 12 to 22 mm ML fed vigorously for several days on postlarval white shrimp (*Penaeus setiferus*) until the shrimp supply ran out (Hanlon *et al.*, 1979).

Larger juveniles and adults (32-285 mm ML) fed vigorously and grew well on shrimps (*Palaemonetes pugio* and *Penaeus* spp.) and an assortment of estuarine fishes including the sailfin molly *Poecilia latipinna*, the sandtrout

Leiostomus xanthurus and all the fishes listed above for *L. opalescens*. Survival on these diets has been relatively high (mean 19 days, maximal 84 days) and growth has been fast (up to 73 mm ML per month) (Hanlon *et al.*, 1978 and in prep.). The field study by Whitaker (1978) on feeding in this species is mentioned above (*L. pealei*).

Doryteuthis bleekeri

Soichi (1976) kept this species for 67 days in a public aquarium. Matsumoto (1976) maintained adults of this species for up to three weeks in an aquarium, feeding them slices of raw tuna and occasionally living goldfish. In later experiments, Matsumoto and Shimada (1980) achieved survival for ten squids of 43-60 days by feeding them thawed pieces of frozen sardines and live goldfish (*Carassius auratus*).

Lolliguncula brevis

This small species is peculiar in its preference for low salinities (Hulet *et al.*, 1979, 1980; Hendrix *et al.*, 1981), which in nature brings it into contact with all the estuarine food organisms listed above that are used to maintain and grow *Loligo opalescens*, *L. plei* and *L. pealei*. No attempts have been made to rear the hatchlings, but on this shrimp and fish diet juveniles and adults (27 to 91 mm ML) survive for comparatively long periods (mean 37 days, maximum 124 days) and grow quickly (mean 10 mm ML/month) (Hanlon *et al.*, 1978 and in prep.).

Lolliguncula panamensis

Squires and Barragan (1979) recorded the stomach contents of this species from trawl samples. They found that 81% of squids with food in their stomachs had pelagic fish remains such as engraulids (*Cetengraulis* spp.) and clupeids (*Opisthonema* spp.). Another 15% had crustacean remains such as the shrimps *Xiphopenaeus riveti* and others.

b. Family OMMASTREPHIDAE

Illex illecebrosus

Bradbury and Aldrich (1969) fed *Illex* on dead capelin (*Mallotus villosus*) suspended on a thread. These authors noted that 'not only will individuals feed, but they will fight for the capelin suspended in their midst'.

Boucher-Rodoni (1975) also used *Mallotus villosus* as food for *Illex* in a study of digestion, but the head, tail and viscera of the fishes were removed before its presentation to the squid.

O'Dor *et al.* (1977) maintained *Illex illecebrosus* in a large tank for 82 days. The squid first fed on live *Fundulus* sp., later on frozen *Fundulus* and on pieces of frozen mackerel, which they captured in midwater. The only male of the group apparently was attacked early in the experiment; it was found dead and half eaten. There was no cannibalism among the females, which became fully mature (see also Amaratunga *et al.*, 1979). In later maintenance and growth studies, O'Dor *et al.* (1980, see also O'Dor, in press) found that *Illex illecebrosus* readily fed upon shrimp (*Crangon* sp.) and a wide variety of small live fishes including capelin *Mallotus villosus*, herring *Clupea harengus*, mackerel *Scomber scombrus*, smelt *Osmerus mordax*, salmon smelts *Salmo salar* and *Fundulus* sp. Vinogradov and Noskov (1979) found that crustaceans were dominant among the prey of *Illex illecebrosus*.

Only very recently have egg masses and hatchlings of known identity been spawned in the laboratory, but all died within eight days and no rearing attempts were made (O'Dor and Durward, 1978).

In view of the small size of the eggs, similar to that of *Illex coindetii* (cf. Boletzky *et al.*, 1973), and the consequently small size of the hatchlings, which are characterized by the fusion of their tentacles ('rhynchoteuthion' stage), one can presume that the newly hatched *Illex* feed on rather small planktonic organisms. It is inconceivable, however, that the 'proboscis' formed by the fused tentacles acts as a pipette, as suggested by Abel (1916). Probably in functional terms the transitory fusion of the tentacles corresponds to the 'press-button' mechanism of the tentacular suckers in adult squid (cf. Boletzky, 1974c). As the fused tentacles have sizable suckers at their tips, it would seem likely that prey of considerable size (in relation to the *Illex* hatchling) are seized with them.

Todarodes pacificus

Mikulich and Kozak (1971) maintained juveniles and adults of this species in aquaria

for periods up to 35 days. Flores *et al.* (1976) found that adult squids could be kept alive for ten days without food, and that they accepted pieces of shrimp and sardine fillet as a regular diet (Flores *et al.*, 1977), with a resulting survival of up to 50 days. Soichi (1976) kept *Todarodes pacificus* for up to 59 days in the aquarium and fed them juvenile mullet and sliced anchovy. Hatchlings of this species have been obtained from egg masses spawned in the laboratory (Hamabe, 1963), but they have not been reared so far. They are very small, similar to the *Illex* hatchlings (cf. above). Records of natural foods of *T. pacificus* have been reviewed by Clarke (1966), the life cycle by Okutani (in press).

Dosidicus gigas

This voracious, active predator seems to prey on nearly any prey available. All feeding information comes from field studies. Fitch (1968) reported that, in the size range of 9 to 50 cm ML, small individuals fed mostly on crustaceans, medium sized squids fed on pelagic fishes (families Engraulidae, Myctophidae, Scorpaenidae, and Embiotocidae), and large squids fed on smaller squids (see also Clarke, 1966).

Nesis (1970) reported that *D. gigas* off Chile and Peru fed upon myctophids (70.2%), squids (13.3%), plankton (7.9%), saury (1.2%) and other unidentifiable foods (7.4%). Sato (1976) reported that *D. gigas* off Baja California fed primarily on the pelagic red crab *Pleuroncodes planipes* but also on myctophid, engraulid and carangid fishes and large quantities of unidentified larvae.

Erhardt *et al.* (MS. presented at work-shop) reported that, in the Gulf of California, *D. gigas* diet consists mainly of sardines (*S. sagax caeruleus*), mackerel (*Scomber japonicus*) and pelagic red crabs (*Pleuroncodes planipes*). From May to July the preferred diet is post-larval penaeid shrimp. Some squids greater than 65 cm ML have been captured with more than 500 g of shrimp larvae in their stomachs! In areas of intense commercial fishing with night lights and jigs, the *D. gigas* feed mainly on their own species.

Hochberg and Fields (1980) stated that *D. gigas* feeds on numerous fishes (anchovies, grunions, skippers, myctophids) and molluscs (pteropods, heteropods, cephalopods). Although *D. gigas* never has been maintained in captivity, it seems possible to keep small individuals in an aquarium. This species is particularly interesting for its very large giant axons. A review of its live cycle is given by Nesis (in press).

Ommastrephes spp.

Clarke (1966) gives a few indications of the stomach contents of *O. pteropus* (fishes, crustaceans, squid hooks) and *O. caroli* (fish and squid remains).

Hixon *et al.* (1980) analysed caecum and stomach contents of *O. pteropus*. Of the filled guts, some contained crustacean carapace remains; these belong to the smaller individuals. Larger animals appear to prey primarily on fishes and on other squids.

Nigmatullin and Pinchukov (1976) found mainly fish and squid remains in the stomachs of *O. bartrami*. This species was more recently analysed by Araya (this volume) who found stomach contents to be mostly fish remains: lantern fishes, sardines, larvae of mackerel and sauries. Squids represented only 18-30% of contents: *Watasenia scintillans*, *Onychoteuthis borealijaponica*, and cannibalised *Ommastrephes*. Planktonic crustaceans (2-18% of contents) were more abundant in young squid as compared to adults; identified crustaceans were members of the Euphausiacea, and *Parathemisto* sp. Consequently Araya (this volume) considered *O. bartrami* as predominantly piscivorous.

iii. Order **OCTOPODA**

a. Family ARGONAUTIDAE

Argonauta argo

This seems to be the only species among the pelagic Incirrata in which feeding has been observed in an aquarium. Lacaze-Duthiers (1892) described a female *Argonauta* which he kept for two weeks in the aquarium of Banyuls-sur-Mer (western Mediterranean). It was fed small living fishes, which it seized very quickly when they came into contact with one of the arms. Young (1960) described feeding experiments using pieces of fish, and Zeiller and Compton (1970) fed an animal brine shrimp and small fishes.

More recently, Boletzky (in press c) kept a female *Argonauta* for one week in a laboratory tank and fed it small crangonid prawns (*Philocheras* sp.) touched to the arms or the mouth, and pieces of shrimp and crab (*Carcinus mediterraneus*); especially portions of crab gonad were touched to the mouth. The animal swallowed these very rapidly using its radula to draw the food in.

b. Family OCTOPODIDAE

All the other laboratory experiments with octopods in which feeding was observed have been made with different species of the benthic octopodid family. In general it is comparatively easy to have the adults feeding on living or dead prey such as crabs, shrimps, bivalves or fishes, and even young octopuses can be raised on a diet of crab meat. In those species, however, that have very small eggs in relation to the size of the adults, the small young hatched from these eggs live for some time in the plankton. Of these, apparently only the hatchlings of *Octopus vulgaris* and *O. ocellatus* in Japan have been reared to the settling stage.

The following species accounts are arranged alphabetically into two groups: the first group includes species with small eggs and small nektonic hatchlings; the second group includes species with large eggs and benthic hatchlings.

Group 1—Small eggs, nektonic hatchlings

Eledone cirrhosa

The hatchlings of this species probably live in the plankton for some time, although they have been found to settle for short periods on hard substrates (Boletzky, 1977). They were fed on half-grown *Artemia*, but did not survive for more than a few days.

Benthic young and adult animals have been maintained in aquaria for many months on a diet of live *Carcinus maenas* (Mangold & Boucher-Rodoni, 1973). Boyle and Knobloch (1981) studied hole-boring by *Eledone cirrhosa* in decapod crustacean carapaces and fed them the crabs *Carcinus maenas*, *Macropipus holsatus*, *M. depurator*, *M. puber*, *Cancer pagurus*, *Corystes cassi velaunus*, *Hyas araneus* and *Pagurus bernhardus*, the shrimp *Crangon vulgaris* and the lobsters *Nephrops norvegicus* and *Homarus vulgaris* (see also Boyle, 1981).

Boyle (in press) summarized the life cycle and reported that *Eledone cirrhosa* also eats eels and probably other fishes as well.

Boyle and Knobloch (1982) studied the growth of juveniles and adults (6 g to 1217 g) fed on a diet of crustaceans, primarily the crabs *Carcinus maenas*, *Macropipus depurator* and *M. holsatus*. Growth on this diet was comparable to other species of octopuses.

Sanchez (1981) described the stomach contents of 171 *E. cirrhosa* caught by trawl in the western Mediterranean Sea. She found that their diet was primarily crustaceans (the shrimp *Alpheus glaber*, the crabs *Gonoplax* sp., *Medeus conchii* and other brachyurans) but also included polychaetes and fishes.

Octopus bimaculatus

Ambrose (1981) observed predation in the field and laboratory and found that *O. bimaculatus* consumed more than 50 prey species from three phyla. Although crabs were clearly preferred, gastropods accounted for 90% of the diet because of the availability in the natural habitat, even though they were the least preferred prey. Shrimps, lobsters, bivalves, chitons and fishes were also consumed, but to a lesser degree. Food preference was determined to be: crabs $\gg$ hermit crabs $>$ bivalves $=$ less motile grazers (e.g. the abalone, *Haliotus* sp.) $\gg$ snails. In summary, this octopus is an opportunistic predator that feeds on a wide size range of organisms.

Octopus burryi

Hanlon and Hixon (1980) fed adult (31 mm ML) and juvenile (13 and 15 mm ML) *O. burryi* the calico crab *Hepatus* sp., the fiddler crab *Uca* sp. and the shore crab *Sesarma* sp. and all were readily eaten. In recent unpublished work Forsythe *et al.* (unpublished data) caught two juveniles in the plankton during night light stations in the Gulf of Mexico and reared one to maturity on a mixed diet of crabs (xanthid mud crabs *Panopeus* sp., hermit crabs *Clibanarius* sp. and fiddler crabs *Uca* sp.) and shrimp *Palaemonetes pugio*. Subsequently a large female (107 mm ML) was caught by trawl; it laid eggs in the laboratory. Forsythe (unpublished data) attempted to rear the small

nektonic hatchlings (1.7 mm ML) in a closed seawater system on live wild-caught copepods, principally *Acartia* and *Labidocera*. The hatchlings fed aggressively, but none lived beyond two weeks and no growth was observed.

Octopus cyanea

Van Heukelem (1976) attempted to rear the nektonic hatchlings of this species, which are similar in size to those of *Octopus vulgaris*. The longest survival was 21 days with hatchlings that were fed combined diets of *Macrobrachium* and *Artemia* larvae. Van Heukelem reported that the newly hatched animals 'began feeding within a few hours of hatching on any appropriate sized crustacean offered. *Artemia* of various sizes from nauplii to adult were attacked and eaten readily as were adult mysids, copepods, and *Lucifer* sp.' (cf. Dew, 1959).

Wells and Wells (1970) fed newly settled (benthic) young of *O. cyanea* 'tiny pieces of fresh bivalve and hermit crab abdomen from the end of a fine wire moved close to the home' of the octopuses. First attacks on small grapsid crabs were observed in the second week. In later weeks the young animals were fed different crabs (grapsids, portunids, xanthids, *Ocypode*), the sand crab *Emerita*, the amphipod *Corophium*, alpheid shrimps and small bivalves (*Ctena bella*, *Macoma* and *Pingua* spp.). Attempts to feed the octopuses on *Littorina scabra* were only partially successful and rather suggested that littorinids are only eaten in the absence of more tasteful food.

Live crabs were used as food for young and adult *O. cyanea* by Yarnall (1969), Boucher-Rodoni (1973) and Van Heukelem (1973, 1976). Van Heukelem (1966) found that xanthid crabs were the principal food of the species on Coconut Island Reef (Hawaii), but he concluded that 'food habits probably depend more on what crabs are abundant in the area rather than selection by the octopus, as the sand-burrowing portunids and *Calappa* were found at lairs surrounded by hard substratum'. Van Heukelem's analysis of crop and stomach contents in animals from a different location revealed, in addition to crab remains, stomatopods, alpheid shrimps, an isopod and fish bones. One animal was captured with a small, paralyzed moray eel in its arms. The life cycle of *O. cyanea* has been reviewed by Van Heukelem (in press).

Octopus defilippi

Grimpe (1928) kept this species in aquaria for several weeks and even months at the Naples Zoological Station. He fed them small crabs of the genus *Pisa* and noted that the octopuses could not readily kill larger crabs. Grimpe further noted that this species survived for short periods on dead shrimp and brachyuran crabs.

Hanlon *et al.* (1980) twice reared wild-caught 'Macrotritopus larvae' to adult *O. defilippi* (from 10 to 90 mm ML in 150 days) on a diet of live fiddler crabs (*Uca* sp.).

Octopus dofleini

This species, known as the giant octopus of the Northwest American coast, has been maintained for long periods in several public aquaria. Gabe (1975) fed adult animals frozen herring (*Clupea* sp.) and large living *Cancer magister* crabs. The nektonic young, hatched in the laboratory, were fed various foods, but accepted only fish fry (*Hemilepidotus hemilepidotus*) and adult *Artemia*. Because of technical problems with the aquarium system, the hatchlings did not survive long.

Marliave (1981) reared the hatchlings to 87 days using nauplii and adults of *Artemia salina*, frozen krill (*Euphausia pacifica*), larval cottid fishes (*Hemilepidotus hemilepidotus*) and trout micropellets. Krill was the preferred food. Marliave (1981) hypothesized that the hatchlings cling to the air-water interface to feed on neuston for the first month in the plankton.

In a field study of adult *O. dofleini*, Hartwick *et al.* (1978) found that they feed almost exclusively on crabs, bivalves and gastropods. Crabs were *Cancer*, gastropods included the moon snail *Polinices lewisii* and the abalone *Haliotis kamchatkana*, and the bivalves included *Chlamys hastata*, *Clinocardium nuttalii*, *Gari californica*, *Hinnites giganteus*, *Humilaria kennerleyi*, *Macoma* sp., *Protothaca staminea*, *Saxidomus giganteus*, *Semele rubropicta*, *Glycymeris subobsoleta*, *Modiolus rectus*, *Mya truncata*, *Mytilus californianus*, *Solen sicarius*, *Tresus* sp., and the brachiopod *Terebratalia* sp.

Hartwick *et al.* (1981) found that octopus

reared in the laboratory or in boxes suspended in the sea fed on live kelp crabs *Pugettia producta* and fillets of dead hake, *Merluccias productus*, in addition to the organisms listed in the previous paragraph (see also Hartwick, in press).

Hochberg and Fields (1980) stated that this species feeds 'on crustaceans (shrimps and crabs), molluscs (scallops, clams, abalones, moon snails, and small octopuses), and fishes (rockfishes, flatfishes, and sculpins).'

Octopus macropus

Taki (1941) reported that *O. variabilis typicus*, which 'is quite allied to *O. macropus*' (and probably falls under synonymy of this species) 'does not feed on living shrimp, stomatopods and crabs, but the bivalve flesh is occasionally eaten', but he noted that fragments of prawn or fish (Gobiidae) were often found in the crop of this species, while pieces of polychaetes were more rarely found.

Voss and Phillips (1957) reported a female *O. macropus* that lived for nearly five months in an aquarium. Feeding was not observed directly, but apparently the animal fed at night on shrimp (*Penaeus* sp.) and small crabs (*Callinectes* sp.) that were regularly supplied.

Hochberg an Couch (1971) noted that this species feeds predominantly on hermit crabs near reefs, and Hanlon *et al.* (1980) noted this species feeding on crabs in a coral rubble area near St. Croix, U.S. Virgin Islands.

Octopus ocellatus

Taki (1941) kept adults in closed seawater systems and fed them the isopod *Lygia exotica* or the bivalve *Venerupis philippinarum*. Yamauchi and Takeda (1964) reared the hatchlings up to 160 g in 229 days. The large, nektonic young (10 mm ML) fed on larval shrimp as well as small (0.2-0.3 g) pieces of dead shrimp meat or *Taper* sp. clam meat until settling on day 10. Until day 70 they were fed minced *Taper* sp. meat. Thereafter (greater than 30 g wet body weight) they ate live *Taper* sp. clams at a feeding rate of about 20 to 30% body weight per day.

Octopus rubescens

Warren *et al.* (1974) used the crab *Hemigrapsus oregonensis* as prey for *Octopus rubescens* in a behavioural study. These authors stated that 'the small animals can be maintained with ease in the laboratory for at least six months, on a diet of 15 to 20 medium-sized rock crabs (shell width 10 to 12 mm; weight 0.2 to 0.5g) per week'.

Hochberg and Fields (1980) report that the adults feed mainly on crustaceans, molluscs and fishes. In the field, small crabs and hermit crabs seem to be preferred. In the laboratory they have been known to drill and eat a variety of gastropods.

Octopus salutii

The hatchlings of this species are much larger (5.2 mm) than those of *O. vulgaris* (2.2 mm), but they have similar body proportions and they are nektonic (Mangold *et al.*, 1976). They feed not only in midwater on small pieces of crab muscle and hepatic gland (as do the hatchlings of *O. vulgaris*), but also on pieces of crab placed on the bottom of the tank (Boletzky, unpubl. obser.). But, these hatchlings have not been reared beyond the first week from hatching. Benthic young and adult animals have been maintained in the laboratory for several months with living *Carcinus maenas* as food (Mangold *et al.*, 1976).

Octopus tetricus

Joll (1976, in press) fed the small nektonic hatchlings of this species on a mixed diet of live *Artemia* nauplii and commercial rice powder preparation ('Farex'); the longest survival was 21 days. Juvenile and adult animals captured from the sea were fed on live crabs (*Portunus pelagicus*), rock lobsters (*Panulirus cygnus*), and mussels (*Mytilus edulis*). In a growth study (Joll, 1977), the octopuses were fed live crabs of *Portunus pelagicus*, *Nectocarcinus integrifrons*, *Leptograpsus variegatus*, and *Plagusia chabrus*.

Octopus vulgaris

Itami *et al.* (1963) reared the nektonic hatchlings of this species to settling and beyond. The newly hatched octopuses, which had a dorsal mantle length of about 2.2 mm, were fed zoea larvae of *Palaemon serrifer* (2-4 mm long), which had been cultured in the laboratory on a diet of *Artemia* nauplii, also added to the octopus tank. In an earlier experiment, the same authors used larvae of *Upogebia maior*

(5-6 mm long) as food for octopus hatchlings, and they reared these to a total length of 6 to 7 mm ML.

When the young octopuses grew to a total length of 6 to 7 mm ML, the early larvae of *Palaemon serrifer* were found to be too small to be caught by the octopuses. At this stage, larger larvae of *Palaemon serrifer* were fed (within 20 days these were reared, using *Artemia* nauplii, to the post-larval stage which has a length of 7 mm ML). When the octopuses approached the 'settling stage', they would sometimes sit on the bottom or the wall of the tank, attaching themselves to the substrate with their suckers, and occasionally they attacked dead food on the bottom. These periods of occasional settling became longer, but the animals still fed primarily in midwater. Definitive settling (which of course does not exclude occasional swimming) occurred between days 33 and 40 of rearing (at temperatures between 22 and nearly 27°C) when the octopuses had attained a dorsal mantle length of about 5 to 6 mm (total length 10 to 13 mm). They were then fed on small pieces (3-4 mm) of ovaries, testes and hepatic glands of the crab *Charybdis japonica.* Three or four days after settling, they were fed on small shrimps and young crabs (*Gaetice depressus*) that had a carapace width of 5 to 7 mm. A young octopus with a total length of 30 mm ML would eat four or five young crabs per day. These octopuses were reared to the age of 90 days.

High mortalities occurred when food was lacking for a few days. Such periods may be bridged with an 'emergency' supply of half-grown and adult *Artemia* that can easily be cultured (cf. Mangold & Boletzky, 1973; Boletzky, 1974a). Young octopuses only a few days after hatching already 'attack' and eat small pieces of crab muscle and gonad that sink from the water surface. Using this feeding method alone, hatchlings have been raised over two weeks, during which time the animals increased considerably in size. In a comparative experiment this food was found to be more readily attacked in midwater than living shrimp larvae of suitable size. Comparatively large pieces of crab muscle (white) or gonad (yellow) sinking from the surface often were attacked by several young octopuses, which generally continued to ingest parts of this food after it had touched the bottom. Octopuses were rarely seen to feed on partly stripped crab legs suspended in midwater. Dark pieces (e.g. of crab gill) never were attacked (Boletzky, unpublished observations).

A large number of different food animals have been successfully used in laboratory work with juvenile and adult *O. vulgaris*. However, if shore crabs such as *Carcinus maenas*, probably the most widely used food for octopus, are available in sufficient numbers and suitable sizes (i.e. carapace width generally not larger than one half of the octopus' mantle length), there is no need for other food items (cf. Nixon, 1969). In the study of the behaviour of *O. vulgaris* in its natural habitat, *Altman* (1967) found 'a wide range of food species, mainly crabs and lamellibranchs', of which she listed four and six species, respectively, together with two gastropod species. The mechanism of hole boring during feeding on molluscan prey has been reviewed by Wodinsky (1969, 1973), with a list of all the mollusc species that have been reported to have holes presumably bored by *Octopus*. The mechanism of hole-boring has been elucidated by Nixon (1979, 1980). Mandibular movements in feeding were analysed by Boyle *et al.* (1979).

Hochberg and Couch (1971) observed *O. vulgaris* on a reef in the U.S. Virgin Islands feeding on the bivalves *Glycymeris decussata*, *G. pectinata*, *Laevicardium laevigatum*, *Arcopagia fausta*, *Artigona rigida* and *Anadara notabilis*, and also on the gastropod *Strombus gigas*, *S. costatus* and *Conus* sp.

Guerra (1978) analyzed the stomach contents of 100 wild-caught *O. vulgaris* (5 to 22 cm ML) in the western Mediterranena Sea. He found that 80% of the diet consisted of crustaceans, 12% of fishes and 8% of cephalopods. In shallow water of 15 to 25 m deep in *Posidonia* sea grass beds, the crustacean diet was 68% shrimps and 32% crabs, while in deeper water of 30 to 80 m the diet was 67% crabs and 33% shrimps. Crustaceans in the diet included: amphipods; the stomatopod *Squilla mantis*; the palaemonid *Palaemon* sp.; the penaeids *Penaeus kerathurus* and *Solenocera membranacea*; the crangonids *Crangon crangon*,

Pontocaris catafracta and *Philocheras* sp.; and the other shrimps *Pandalina brevirostris*, *Alpheus* sp. and *processa* sp. Brachyuran crab species included *Dromia personata*, *Ethusa mascarone*, *Dorippe lanata*, *Calappa granulata*, *Macropipus* sp., *M. corrugatus*, *M. depurator*, *Carcinus mediterraneus*, *Goneplax rhomoides*, *Pisa nodipes*, *P. armata*, *Inachus* sp. and *Pachygrapsus* sp. Anomuran crab species included *Anapagurus laevis*, *Anapagurus* sp., *Galathea* sp. and *Pisida longicornis*. Cephalopod prey included *Loligo vulgaris*, *Sepia* sp. and *Octopus* sp. Fish remains included *Cepola rubescens*, *Uranoscopus* sp., and unidentified clupeids.

Nigmatullin and Ostapenko (1976) analyzed the diet of 2 025 *O. vulgaris* from the north-western coast of Africa and found predominantly crustaceans (53.6%), followed by fishes (25.5%), molluscs (9.5%), and other *O. vulgaris* (7.5%).

The preference for a crab diet, already noted by Taki (1941), is again emphasised by Altman and Nixon (1970; see also for reference list on feeding behaviour). These authors also noted that an all fish diet, often used as standard reward in behaviour experiments, causes a colour change of the digestive gland from the normal orange colour to an olive-green colour that is never observed in animals freshly captured from the sea. It may finally be noted that attempts to substitute other food items for the natural prey of *Octopus* have been made long ago. Vlés (1914) found that octopuses readily accepted chicken eggs, fresh ones as well as hard-boiled rotten eggs!

Octopus vulgaris is regularly kept in certain inland aquaria (cf. Vevers, 1962). It is one of the most widely used cephalopods for experimental studies (Wells, 1978). Mangold (in press a) reviewed the life cycle.

Pteroctopus tetracirrhus

Boletzky (1976) maintained subadult and adult animals of this species over periods of four to nearly five months in aquaria. The octopuses were fed mainly *Carcinus maenas* (claws removed), and occasionally *Leander serratus*, *Lysmata seticaudata* and *Nephrops norvegicus* (see also Boletzky, 1981).

Group 2 — Large eggs, benthic hatchlings

In contrast to the preceding species, the hatchlings of the following octopods are fairly large relative to the adult size, and they remain benthic from hatching onwards. The feeding habits of the hatchlings are similar to those of the adults, and it is not surprising that rearing them from hatching is easier than rearing nektonic young to the stage where they change to a benthic mode of life.

Bathypolypus arcticus

Macalaster (1976) maintained two animals in the laboratory over several months. They accepted a wide variety of prey species, the most common of which were polychaete worms, amphipods (*Gammarus* spp.) and other small crustaceans.

The analysis of stomach contents in 450 specimens captured in the Newfoundland area revealed that the following groups were represented in the diet of *Bathypolypus arcticus*: ophiurids, crustaceans, polychaetes, bivalves, gastropods, foraminifers, sipunculids and cumaceans. Macalaster concluded that '*B. arctictus* is probably not selective, but opportunistic in its choice of prey'. O'Dor and Macalaster (in press) reviewed the life cycle.

Eledone moschata

Boletzky (1975b) reared the large benthic hatchlings of this species to the adult stage. During the first two months, the young animals were fed small pieces of shrimp (*Leander* spp.) and crab (*Carcinus maenas*). Later on they regularly fed on small living crabs (generally *Carcinus maenas*). The young animals usually pounce upon living and dead prey, but they also accept food that is touched to them or that is simply placed on the bottom of the tank. More recently, feeding experiments have shown that young *E. moschata* are able to capture the small crangonid *Philocheras* spp., although often many attacks are necessary as this prey may escape by very rapid leaps.

In another rearing experiment (Boletzky, unpublished data), *E. moschata* was reared entirely on pieces of fresh crab. Growth was slower with this diet. In the earlier experiment (Boletzky, 1975b) the males were not sexually mature at the age of one year, whereas the

females were spawning at ten months of age. In the later experiment, where growth was slower, the smallest males became sexually mature together with the females, larger males one to two months later. Finally a batch of animals was severely underfed from hatching onward, and under these conditions the females became mature *after* the males (see also Mangold, this volume and Mangold, in press b).

Hapalochlaena maculosa
(= *Octopus maculosus*)

In contrast to the somewhat larger species of blue-ringed octopus, *H. lunulata*, which has small eggs (3.5 mm long) and hatchlings (2.3 mm ML) and first lives in the plankton (Overath & Boletzky, 1974), the eggs (6-7 mm) and hatchlings (3.5-4.0 mm ML) of *H. maculosa* are large relative to the adult and live on the bottom. These large young have been cultured by Tranter and Augustine (1973), who found that the hatchlings 'showed little interest in food until about one week after hatching, by which time the more vigorous ones were beginning to attack and eat the less vigorous ones. They then began to accept pieces of crab meat and soon welcomed such rations daily'. Live crabs (*Chasmognathus laevis*, *Sesarma erythrodactyla*, *Heloecius cardiformis*) were attacked and eaten only by octopuses at least four weeks old: 'At first they would attack only crabs smaller than themselves, but later, particularly when they were hungry, they would kill and devour larger ones'.

Octopus australis

Tait (1980) found that this species readily ate the live grapsid and portunid crabs *Paragrapsus quadridentatus*, *Cyclograpsus audounii*, *C. granulatus* and *Carcinus maenas* in the laboratory. His analyses of stomach contents of wild-caught specimens indicated that crustacea, predominantly isopods, constitute most of the diet. Other crustacean remains represented the Amphipoda, Tanaidaea, Mysidaea and Cumacea. Molluscan remains included bivalves, gastropods and octopods. A few stomachs had polychaete worm remains.

Octopus bimaculoides

Hochberg and Fields (1980) reviewed the existing literature on this species and they stated that the adults feed on molluscs, crustaceans and occasionally fishes. In the rocky intertidal zone it feeds on various limpets (*Collisella* sp. and *Notoacmea* spp.), the black abalone *Haliotis crachecrodii*, the snails *Olivella biplicata*, *Tegula funebralis* and *T. gallina*, the clam *Protothaca staminea* and several hermit crabs of the genus *Pagurus*. In mud flat regions it feeds on the bivalves *Chione undatella*, *Mytilus edulis*, *Leptopecten monotimerus*, and *Argopecten aequisulcatus* and it sometimes captures the small blennies *Hypsoblennius gilberti* and *H. gentilis*. In subtidal waters it feeds on the abalones *Haliotis rufescens*, *H. fulgens* and *H. corrugata*, the snails *Kelletia kelletii*, *Astraea undosa* and *Norrisia norrisi*, and the hermit crab *Paguristes ulreyi*. They state that under laboratory conditions this octopus will eat almost any shelled mollusc.

Borer (1970) analysed food intake in *O. bimaculoides* using shore crabs, *Pachygrapsus crassipes*, as food.

Octopus briareus

Messenger (1963) fed the comparatively large hatchlings of *O. briareus* on pieces of freshly killed shrimp touched to them and on live crustaceans of small size (less than 10 mm in length), namely *Latreutes fucorum*, *Leander* sp., *Hippolyte* sp. and some unidentified amphipods, and on young and adult *Artemia*. Messenger observed that 'the animals always seized the prey with a few arms and anchored themselves with the remainder. They never swept down on the prey like adult octopuses and indeed many feedings were the result not of an attack by the octopus, but of the prey accidentally entangling itself with some of the arms'.

Wolterding (1971) fed the hatchlings of *O. briareus* on disarticulated legs of adult fiddler crabs (*Uca pugilator*). These legs were placed at the end of a long glass needle 'and lowered toward the octopus, which grabbed the food and drew it off the needle'. Wolterding noted that 'after two weeks, young *O. briareus* begin to feed on very small *Uca pugilator*, amphipods and majids'. Leg segments of adult *U. pugilator* were given along with the live food for two more weeks. Larger animals were presented with about 65 species of polychaetes,

echinoderms, crustaceans and fish. Some were actively attacked but not eaten, while others were not attacked but were eaten when coming into contact with the octopus. Cannibalism occurred on other *O. briareus* as well as on *O. joubini*.

The following species were found to be eaten (being or not being actively attacked): polychaetes: *Hermodice carunculata*, *Onuphia magna* (without tube), *Chaetopterus variopedatus* (with tube); crustaceans: *Leander tenuicornis*, *Tozeuma carolinense*, *Hippolyte* sp., *Penaeus duorarum*, *Synalpheus brevicarpus*, *Alpheus formosus*, *Panulirus argus*, *Gonodactylus* sp., *Portunus* spp., *Callinectes sapidus*, *C. ornatus*, *Aratus pisonii*, *Grapsus grapsus*, *Pachygrapsus transversus*, *Cardisoma guanhumi*, *Gecarcinus lateralis*, *Calappa flammea*, *Mennippe mercenaria*, *Panopeus herbstii*, *Sesarma cinereum*, *Ocypode albicans*, *Libinia erinacea*, *Mithrax hispidus*, *Stenorhynchus seticornis*, *Macrocoeloma*, sp., *Emerita talpoida*, *Coenobita clypeatus*, *Clibinarius tricolor*, *C. vittatus*, *Dardanaus venosus*, *Petrochirus digenes*; fishes: *Scorpaena brasiliensis*, *Opsanus beta*, *Acanthostracion quadricornis*, *Hippocampus erectus*, *Trachinotus carolinus*.

Wolterding noted that 'all crabs up to a size equal to that of the octopus were actively attacked'. Echinoderms were not eaten by *O. briareus*. The only molluscs eaten were other octopuses, as mentioned above; neither gastropods nor bivalves were eaten.

Borer (1971) used the fiddler crab, *Uca pugilator*, as food in all experiments except one on the control of food intake in *Octopus briareus*. In one experiment, stone and mud crabs (*Panopeus herbstii*, *Eriphia gonagra*, and *Micropanope nuttingi*) were used in addition to fiddler crabs.

In a study of growth in *O. briareus*, Hanlon (1975) fed some hatchlings on very small live *Uca pugilator* (3-8 mm carapace width) and others on crab legs and pieces of shrimp that were placed with fine forceps into the arms of the octopus hatchlings. Hanlon found that 'one small shrimp *Penaeus duorarum* (60 mm long) is adequate for feeding 150 hatchlings'. *Artemia* was used only as a supplementary food source. Larger octopuses were also fed on blue crabs (*Callinectes*) and on shrimp (*Penaeus duorarum*, *P. aztecus*, *P. brasiliensis*) (see also Hanlon, 1977).

In recent experiments Forsythe and Hanlon (unpublished data) reared this species primarily on live shrimps but also on crabs and fishes *Fundulus similis*, *Mugil cephalus* and *Menidia berylline*. The methods and prey organisms were identical to those used earlier (Forsythe & Hanlon, 1981) and the growth rates on a shrimp diet were comparable to those obtained on a crab diet. At the Dallas Aquarium, *O. briareus* has been fed live freshwater crayfish (*Cambarus* sp.). Hanlon (in press, b) reviewed the life cycle.

Octopus joubini

This species, like the preceding one, has eggs very large (8 mm long) in relation to the adult, and the hatchlings are benthic and can be reared rather easily. Most workers fed them a diet of crab legs and/or small crabs of the genus *Uca* (Boletzky & Boletzky, 1969; Thomas & Opresko, 1973; Opresko & Thomas, 1975; Forsythe & Hanlon, 1980, 1981; Forsythe, 1981).

Several other prey organisms have been used. Bradley (1974) used crab meat and small living shore crabs of *Carcinus maenas*. Mather (1972, 1980) investigated the predatory behaviour and feeding of *O. joubini* using *Uca pugilator*, the hermit crab *Pagurus pollicaris* and the gastropod *Nassarius vibex* as prey. She found that the shells of the snails that had been eaten showed no sign of drilling (cf. Wodinsky, 1969, 1973). Thomas and Opresko (1973) noted that gammarids, caprellids and various other amphipods as well as isopods were rejected by the young octopuses, as generally were *Artemia*. Forsythe and Hanlon (1980) reared *O. joubini* primarily on *Uca* spp. and xanthid mud crabs, but found that small penaeid shrimp *Penaeus* spp., palaemonid shrimp *Palaemonetes pugio* and mysid shrimp *Mysidopsis almyra* were accepted though less preferred by the octopuses. They also found that the small marine amphipod *Orchestia grillis* was accepted readily by octopus hatchlings and 'seems to be as acceptable a live food as small crabs'. They found that dead food such as crab, fish or shrimp meat was accepted only reluctantly, but could be used to

maintain adult octopuses temporarily if no live food were available.

In the most recent experiments (Forsythe & Hanlon, 1981) *O. joubini* was reared to sexual maturity on a diet composed exclusively of live mysidacean and caridean shrimps (*Mysidopsis almyra* and *Palaemonetes pugio*). Survival and growth rates were comparable to previous rearing studies that used live decapod crabs (Forsythe, 1981) and showed that the more easily collected and available shrimps were reliable food alternatives for rearing *O. joubini.*

This species has been reared several times in inland aquaria (Bradley, 1974; Overath, pers. comm., 1975; Forsythe & Hanlon, 1980). The life cycle is reviewed by Hanlon (in press a).

Octopus maya

Solis (1967) reared the large benthic hatchlings of this species to the age of 76 days, using mainly small crustaceans as food.

Van Heukelem (1976, 1977) fed the hatchlings of *Octopus maya* bits of frozen crab meat and viscera, frozen shrimp (*Heterocarpus ensifer*), frozen *Artemia*, live *Artemia* nauplii, juvenile and adult *Artemia* reared on yeast and phytoplankton, live gammarid and caprellid amphipods, isopods, and a variety of zooplankton. Feeding on frozen food resulted in slower growth and higher cannibalism than feeding on living prey. Larger animals, weighing more than 10 g, were fed xanthid crabs. Octopuses weighing more than 500 g were fed primarily on the crab *Podothalmus vigil* but were given *Portunus sanguinolentus* or *Thalamita cranata* when supplies of *P. vigil* were insufficient. Two to four month old octopuses accepted gastropods (*Littorina* sp. and *Cypraea caputserpentis*) and clams (*Tapes* sp.), but they would not eat these molluscs if living crustaceans were present. This octopus species was cultured through four generations. Van Heukelem (in press) reviewed the life cycle of *O. maya*.

C. ARTIFICIAL DIETS AND CEPHALOPOD MASS CULTURE

The earliest successful attempts to rear cephalopods opened a new line of aquacultural prospects. In the summary of his report 'On the Growth, Feeding Rates and the Efficiency of Food Conversion for Cuttlefishes and Squids', Choe (1966b) concluded that 'four to five months are thought to be enough for their growing into a fair commercial size'.

However, fifteen years later, neither cuttlefishes nor squids have made their breakthrough in aquaculture. In 1977, Egusa (pers. comm.) described the situation in Japan as follows: '*Octopus vulgaris* is the only cephalopod commercially reared in Japan. Its annual production of reared animals has been about 50 tons in recent years (about 100 tons 1967-1971). The main foods are horse mackerel, saury, and other trash fish, whose food conversion factors are said to be 2.5 to 5.0. No work has been done on artificial foods for this octopod. There are only two reports on the experimental culture of *O. vulgaris* hatchlings (Itami *et al.*, 1963) and of *O. ocellatus* (Yamauchi & Takeda, 1964). In these experiments live crustaceans, molluscs, and fishes were used as foods, no attempt being done on artificial diets. Ever since no scientific report has been published on the culture of octopods'. He concludes: 'Cephalopod young are very selective feeders, requiring live animals of suitable size, and a great difficulty lies inevitably in obtaining food animals in large quantities needed for the mass culture of cephalopod larvae. The success of the mass culture seems to depend entirely on the development of synthetic food'.

Van Heukelem (1976) suggested that 'of all cephalopods raised in captivity to date, *O. maya* appears to be the best candidate for mariculture', and he emphasised that 'difficulties to be overcome before large scale, economical production could be achieved include development of a cheap, easily storable food. I have no doubt that this could be achieved in a short time by an experienced fish culturist with a good background in nutrition and a fair amount of insight'. Indeed the essential dietary constituents will have to be determined and made available in an acceptable form, e.g., enough copper must be included because cephalopods depend on it for their haemocyanin synthesis (cf. Ghiretti & Violante, 1964).

In view of the increasing demand for cephalopods on the markets of Oriental and Latin

countries (Voss, 1973, 1974), the development of a standard 'pellet food' for octopods, with the corresponding method of presentation, would seem to be an urgent goal. But although the raw material for such food would be available, in large quantities from fish and shrimp processing plants and canneries, transformation of this raw material into cheap storable food for octopods still awaits realization.

Discussion

A tabular presentation of culture data clearly shows that many more cephalopod species have been maintained or reared in captivity (20 genera, 52 species; Tables 1 and 2) than have actually been cultured through whole generations (7 genera, 11 species; Table 3). The large majority of those species that have been cultured in the laboratory are benthic, only one is nektonic (*Loligo opalescens*). Culture of cephalopods through the life cycle must therefore be regarded as being in the early stages of development, particularly as compared to the advanced culture development of finfishes, shelled molluscs or penaeid and palaemonid shrimps. The review of diets indicates that cephalopods are carnivores that feed on a wide size range and variety of life food organisms, primarily crustaceans, shelled molluscs, fishes and other cephalopods.

Clearly many cephalopods are adaptable, to some degree at least, to maintenance and rearing work. The relatively small proportion of cephalopods that has been kept in the laboratory (i.e. approximately 52 species of more than 700 in the Class Cephalopoda) is mostly a reflection of the lack of work on cephalopods. Certainly many more are amenable to maintenance or rearing, especially the benthic sepioids and octopuses. Several active pelagic squids of commercial importance have been maintained or reared for months, as shown by the recent works on *Todarodes* (Flores *et al.*, 1976, 1977), *Illex* (O'Dor *et al.*, 1980) and *Loligo* (Hanlon *et al.*, 1980 and in prep.; Hixon, 1980). It is encouraging that even delicate midwater squids such as *Abraliopsis* sp., *Pyroteuthis addolux*, *Heteroteuthis hawaiiensis*, and very strong pelagic swimmers such as *Symplectoteuthis oualaniensis* can be captured and maintained in captivity at least for hours or days (Young and Roper, 1977; Young *et al.*, 1979a,b). These achievements set the stage for improvement of techniques that satisfy the four basic requirements of successful maintenance, rearing or culture work:

(1) atraumatic collection and transport of live embryos, juveniles, or adults at the outset of culture
(2) high quality sea water
(3) sufficient tank space to accommodate the benthic or nektonic mode of life as well as distinctive behavioural traits
(4) appropriate type and quantity of live food

Future prospects for culture (*sensu stricto*) are more limited than those of maintenance and rearing, but recent substantial advances indicate good future potential. Culture of species with large, benthic young (e.g. *Sepia officinalis*, *Octopus maya*) is an established, straightforward enterprise (cf. Table 3), and those basic techniques are surely applicable to other species. Studies on *Octopus vulgaris* by Itami *et al.* (1963) and on *Loligo opalescens* by Yang *et al.* (1980b, in press) provide the essential techniques for species that have nektonic young, but they also highlight the fact that such studies are labor intensive, expensive and time consuming. Food is by far the problem of overwhelming importance, and this aspect of culture must be addressed vigorously in order to refine and simplify techniques.

The following sections briefly sum up the data in this review and our suggestions for future investigation. We begin by stating the most obvious gaps in our knowledge, then continue with the desirable attributes of candidate species and the theoretical and practical limitations of studying them, and we conclude by stressing the importance of rapid exchange of information among cephalopod biologists.

A. GAPS IN OUR KNOWLEDGE

Clearly one of the most crucial conditions for successful culture work is the healthy state of the animals at the outset of an experiment. If the experiment is begun by collecting juvenile or adult cephalopods in the sea, atraumatic

TABLE 3

Cephalopod species that have been cultured at least to the first filial generation in the laboratory.

Order	Family	Species	Mode of life of young animals	Mean mantle length at hatching (mm)	Approximate adult size at reproduction (mm ML)	Maximum time in culture (days)	Number of generations	Type of seawater system	Reference
Sepioidea	Sepiidae	Sepia officinalis	benthic	8.0	70 - 250	420	2	closed	Schröder, 1966
		" "	"	"	"	500	"several"	open	Richard, 1966, 1971, 1975
		" "	"	"	"	730	1	open	Boletzky, 1979b
		" "	"	"	"	609	3	open	Pascual, 1978
		" "	"	"	"	1,800	5	open	Zahn, 1979; pers. comm. 1981
	Sepiolidae	Sepiola affinis	benthic	3.2	20	250	1	open	
		Sepiola robusta	"	2.2	20	220	1	open	Boletzky, et al., 1971; Boletzky, 1975c
		Sepiola rondeleti	"	3.7	20	150	1	open	
		Sepietta oweniana	"	~ 5.0	30 - 40	~ 300	1	open	Summers & Bergstrom, 1981
Teuthoidea	Loliginidae	Loligo opalescens	nektonic	2.7	85	233	1	closed	Yang et al., 1980, 1982; Hixon et al. (in prep)
Octopoda	Octopodidae	Octopus briareus	benthic	7.0	90	500	1	open	Wolterding, 1971, 1981
		Octopus joubini	benthic	3.3	25	510	4	open	Thomas & Opresko, 1973; Opresko & Thomas, 1975
		Octopus joubini	benthic	5.0	30	240	2	closed	Forsythe & Hanlon, 1980, 1981; Forsythe, 1981
		Octopus maya	benthic	7.0	100	1,100	4	open	Van Heukelem, 1976, 1977
		Eledone moschata	benthic	10.0	100	380	1	open	Boletzky, 1975b
		Hapalochlaena maculosa	benthic	4.0	35	360	2	open	Tranter & Augustine, 1973

procedures of capture and transport are particularly important. Although certain generalizations may be possible for some cephalopods, species-specific characteristics of behaviour must be taken into account for the choice of collection methods. For example, not all squid species react similarly to specific capture methods (seine, night light, dipnet, jig), and the method of greatest consistency and effectiveness will have to be determined. Transport requirements also must be defined precisely for each species. The advantages and drawbacks of anaesthesia during transport are largely unexplored.

One of the greatest gaps in our knowledge of cephalopod life history concerns the early juvenile phase of nektonic species. What are the optimum conditions for survival and growth of hatchlings and juveniles in captivity, especially as related to water movement, light conditions, food types and food densities? The types of food attractive to young nektonic cephalopods are live copepods, larval crustaceans and larval fishes that have an erratic swimming motion. The sizes of food that hatchlings and juveniles attack range widely from less than ⅓ to more than double the mantle length of the cephalopod, but it remains to be determined which types and sizes of food organisms meet the behavioural and nutritional requirements of different cephalopods. Probably the optimum density of food organisms is a function of the type of food offered; indeed finding the density that promotes optimal feeding with a given prey type is of particular importance. Certain types of live prey may not be favorable to cephalopod growth at all. Unfortunately this is true with the most easily cultured food organism, the brine shrimp *Artemia* spp. A possible alternative to be investigated is the palaemonid shrimps that can be cultured through their life cycle, so that larvae, juveniles and adults can be used as prey suitable for all growth stages of cephalopod predators (cf. Itami *et al.*, 1963).

For larger juveniles and adults, substitution of natural prey by an artificial food ration is conceivable, but the entire complex of features required to make such food acceptable to a cephalopod predator remains to be studied (e.g. size, texture, taste, visual stimuli, including outline and movement of the 'prey'). On the positive side there exists the possibility of behaviourally conditioning the cephalopod predators to feed on artificial foods (cf. Boletzky, 1972).

Sensory and reproductive physiology must be studied from the viewpoint of maintaining, rearing or culturing cephalopods in an artificial, confined environment. Aspects of social behaviour, particularly territoriality, intraspecific aggression and cannibalism, are serious restraints in keeping some species in captivity. Aspects of sexual maturation can be important limitations in the culture of many species, especially regulating factors and behavioural and physiological changes that accompany them. Since laboratory conditions are poor representations of the natural environment, study should be directed at determining the appropriate 'sensory input' (cf. Blaxter 1970) necessary for normal behavioural and physiological development.

The problems of parasites and diseases in cephalopod culture are only beginning to be recognized. They may become of major importance when large-scale or intensive culture is undertaken, and methods of prophylaxis must be developed.

Finally, there is a significant dearth of information on the habits and the commercial and scientific value of most of the 700 or more species of cephalopods that are known to exist. Many of them undoubtedly hold future promise as being useful and important to man, and no one should ever be discouraged from making preliminary observations of these species under laboratory conditions.

B. CANDIDATE SPECIES AND LIMITATIONS

The choice of species depends largely upon the purpose of the investigation. Commercially important species will be studied in the context of fisheries biology, or the species will be chosen to provide experimental material such as squid giant axons. If possible, initial work should be set up with species that are easily available from local stocks.

Each of the following attributes of a candidate species should be carefully reviewed: (1) egg size and resulting size of hatchlings, (2)

mode of life of hatchling, especially of octopuses (does it correspond to the adult mode?), (3) numbers of offspring per female, (4) food requirements, (5) growth rates, (6) time to sexual maturation, (7) activity and behaviour, and possibly (8) tolerance to operative techniques. Whenever such information is not available from the literature, personal consultation with those who have observed or studied the species is advisable. Fishermen often are a particularly good source of information on general aspects of occurrence and life history.

In addition to the aforementioned theoretical limitations of choosing a species, there are practical limitations to consider. In most cases, very large facilities are too expensive, so that maintenance or culture of very large species become prohibitive. For many purposes in basic and applied research, small species are useful models, but they cannot always answer the questions relating specifically to larger species.

For a given animal size, difficulties are always greater with actively swimming animals than with the bottom-living species. This applies in particular to density limitations. Bottom-living cephalopods need minimum horizontal areas that have been estimated at ten times the body surface area in cuttlefishes (Richard, 1975) or more generally as $(5 \times ML)^2$ for most benthic cephalopods that are not territorial (Boletzky, 1974a). Water depth is less important for benthic animals, whereas actively swimming cephalopods generally need greater water depths in addition to horizontally wider space.

Apart from space requirements, adult size of animals has its implications in the time scale of rearing and culture work. Small species like *Octopus joubini* and *Sepiola* spp. are sexually mature four to five months after hatching. According to the length of embryonic development, which varies with temperature, the entire reproductive cycle of these species covers only six to eight months. With very large species, the minimum duration of one reproductive cycle is always more than one year, sometimes two years or more. Even medium-sized cephalopods like *Eledone moschata* have a reproductive cycle covering more than one year, especially when they have very large eggs that need several months for embryonic development. For a review of cephalopod life cycles consult Boyle (in press).

These aspects have to be taken into account when a rearing or culture program is planned, because for a given volume of culture space, the 'output' per unit time decreases drastically with increasing adult size of the animals. Adult size as such can be kept in limits to a certain extent. Indeed food intake often decreases under culture conditions, either for lack of an optimal choice of food organisms or for other reasons like disturbance of normal activity cycles or general sensory deprivation. Experiments with *Eledone moschata*, reported in this article, and with *Sepia officinalis* (Boletzky, 1979b) show that 'dwarfed' individuals can live and behave normally, reach sexual maturity and reproduce. These results have important practical and theoretical consequences. On the practical side, they show that rather large species like *Sepia officinalis* need not attain the normal adult size to be useful as experimental animals, for example in physiological or behavioural long-term experimentation. On the theoretical side, they draw attention to the considerable physiological flexibility of many cephalopods that are able to adapt to highly artificial conditions. We do not know if cultivation increases behavioral or morphological variation, which in turn may dramatically affect their suitability as experimental animals.

C. INFORMATION FLOW

In spite of modern communication systems, exchange of information often is slow. Considerable time can be lost in 'trial and error' approaches to culture, when in some instances the technology already exists and need only be communicated to the experimentor. The present review attempts to present the state of the art as it appears to us in 1981/82. More recent information in culture, especially unpublished data and suggestions, would have been helpful in updating this review, and we solicit such information for the future. Written information should periodically be complemented by personal contacts between the people actually involved in one or several of the very many aspects related to cephalopod culture. The first

International Workshop on the Biology and Resource Potential of Cephalopods held in Melbourne and Queenscliff in March 1981 provided an excellent example of using personal contact to provide interdisciplinary coverage of the particular problems of Australian squid fisheries.

To learn the complex interrelationships of cephalopods in their natural environment it is necessary to maintain information feedback between the fisheries biologist (with his broad approach) and the culturist (with his reductionist approach). For example, age determination, which can be provided by laboratory culture, is one of the key problems in all attempts to describe the dynamics of a natural population. The possible use of periodic structures such as 'growth rings' of statoliths was discussed at this workshop first from the practical viewpoint of routine aging of specimens sampled in fishery biology, and second under the more fundamental aspect of cyclic processes in growth. Culture work is necessary to provide detailed insight into cephalopod life cycles; conversely, fisheries investigation provides stimulating insights into spatial and numerical dimensions of population dynamics that cannot be reconstructed under culture conditions.

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A REVIEW OF THE BIOLOGY OF THE OCEANIC SQUID *ONYCHOTEUTHIS BOREALIJAPONICA*

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Abstract

A part of the migrating population of *Onychoteuthis borealijaponica* has been utilized as an incidental catch of conventional commercial species. It propagates in the southwestern waters of Japan and feeds and matures in the cold water area off Hokkaido. At maturity females attain a length of 32 cm ML and an ovarian weight of 78 g. Spermatophores are implanted in cuts on the ventral mantle of the females. Substantial catches of this species are taken in water at temperatures of 5°C to 20°C when the squid undertake a south-north migration. An attempt is made to estimate the potential yield of this squid.

Introduction

The oceanic squid, *Onychoteuthis borealijaponica* Okada, 1927‡, was reported to be available in the market in Hokkaido (Sasaki, 1929), and recently has become more popular. This species constitutes an incidental catch of the fishery for the Japanese common squid, *Todarodes pacificus* Steenstrup. At present, the *O. borealijaponica* population is being partially exploited due to the depletion of the *T. pacificus* stock, and recent exploitation of *Ommastrephes bartrami* (Lesueur) to the east of Hokkaido (Table 1).

Table 1

Catches of *O. borealijaponica* landed in northeastern Honshu and Hokkaido.

Year	Catch in tons
1971	2 232
1972	750
1973	60
1974	5 060
1975	0
1976	2 225
1977	54
1978	77
1979	89

This paper reviews the recent contributions to the ecology of *O. borealijaponica* principally from the fishery-biological point of view.

‡ This species had not always been separated from *O. banksi* (Leach) before this name was revived by Young (1972).

1. *Juvenile Distribution.* Identification of *O. borealijaponica* and *O. banksi* is almost impossible in the very early stages of life. Planktonic juveniles of *Onychoteuthis* found in the northwestern Pacific Ocean, including Japanese waters, are thought to belong to the former species on the basis of morphological sequences which lead to identifiable specimens of advanced age.

Of the 2 002 epipelagic squid juveniles collected by 355 surface horizontal tows off the Pacific coast of western Japan, only 8 (0.4%) were identified as *O. borealijaponica* (Okutani, 1968). In contrast, 22 (1.4%) specimens were identified among 1 543 squid juveniles collected with 110 depth-discrete tows at 20 m, 50 m, 100 m and 200 m, in the seas around Ryukyu Islands, southwestern Japan (Yamamoto and Okutani, 1975). This seems to suggest that *O. borealijaponica* reproduces in the mid-layer of the ocean but not in the surface layer. In connection with this, 132 juveniles (3.8%) of this species were discovered among 3 429 squids collected with CalCOFI tows from the surface to a depth of about 150 m in the California Current (Okutani & McGowan, 1969). The greatest depth reported for a juvenile of *O. banksi* in the North Atlantic is 1 000-1 250 m (Clarke & Lu, 1974). The vertical distribution of *O. borealijaponica* is not known.

The population of *O. borealijaponica* around the Japanese Islands appears to make a north-south migration. The juvenile population is distributed exclusively in the warm water area off southwestern Japan (Kuroshio and the

countercurrent areas). Adults are commercially exploited in the cold water area off Hokkaido (Subarctic and mixing water areas) where they feed, grow and mature.

2. *Growth and Maturity.* The fishing season for *O. borealijaponica* to the east of Hokkaido lasts from spring (April-June) to fall (October). The mantle length range of jigged specimens is 10-36 cm in females and 11-28 cm in males. The size range of the major constituents varies by season and by year (Figure 1). The mantle

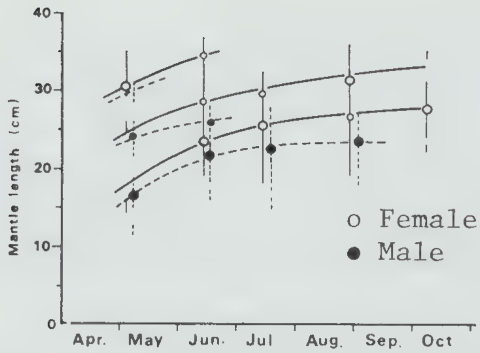

Figure 1. Seasonal change in mantle length for the 1976 catch (from Naito *et al.*, 1977).

length composition usually shows a unimodal distribution but sometimes is bimodal. The example shown by Murata and Ishii (1977) is females 17-22 cm and 25-30 cm in the 1968, 1973 and 1975 fishing seasons. The regression lines for mantle length (L) against body weight (W) obtained by them are: $W=3.6089\times10^{-5}L^{2.896}$ (female, $R=0.9861$, $N=623$) and $W=1.4073\times10^{-4}L^{2.627}$ (male, $R=0.9600$, $N=208$). The body weight of the female is 6-12% greater than the male at the same mantle length (Figure 2).

Nidamental gland length and ovarian weight have been used as indicators of sexual maturity in females. In June, during the early period of occurrence on the fishing ground, the mode of nidamental gland length is 2-3 cm, while later in August-October, it becomes 4-6 cm, showing an advancement of maturity with time. This corresponds to an increase of ovarian weight from 1-5 g in June to over 5 g after August, although a great variability among specimens exists. The increase of ovarian weight is proportional to that of mantle length up to 27-28 cm, but the ovarian weight shows an abrupt rise thereafter (Figure 3). The greatest value of ovarian weight reported by Murata and Ishii (1977) is 78.0 g for 32.3 cm mantle length. In fully mature females, namely, those with nidamental gland lengths between 6 and 10 cm and ovarian weights over 20 g, the genital organs are orange in color. The change in pigmentation starts at the genital opening then proceeds to the ovary and finally covers the nidamental gland and inner wall of the mantle.

It is well known that onychoteuthids do not possess a hectocotylized arm. A single female jigged at 43°02′N, 148°50′E on August 29, 1976, carried sperm masses implanted in the tissues of the ventral mantle (Murata & Ishii, 1977). This specimen had a cut, 67 mm long, 2 mm wide and 5 mm deep, in the ventral midline near the anterior end. This condition is similar to what Clarke (1980) described for another onychoteuthid, *Moroteuthis robsoni*. Such cuts seem to be used for implantation of spermatophores.

Murata and Ishii (1977) found that males taken during June to September were mostly sexually mature except for specimens smaller than 20 cm mantle length. Half of the males in the June catch had a testis weight between 10 and 17 g which dropped to less than 10 g in September. This drop is attributed to loading of spermatophores in the spermatophore sac as well as to consumption through copulatory activity. On the basis of the relationship between testis weight and weight of Needham's sac, advancement and decline of male genital organs from June to September is quite evident. The numbers of spermatophores carried by a single male ranged from 10-20 to 70-80.

Naito *et al.* (1977b) reported that females mature later than males like the oceanic ommastrephids *Ommastrephes bartrami* and *Todarodes pacificus*. A disappearance from the fishing ground east of Hokkaido after the fall may signal the start of the southward migration for spawning. With time, the sex ratio of the population changes. In June-July, when

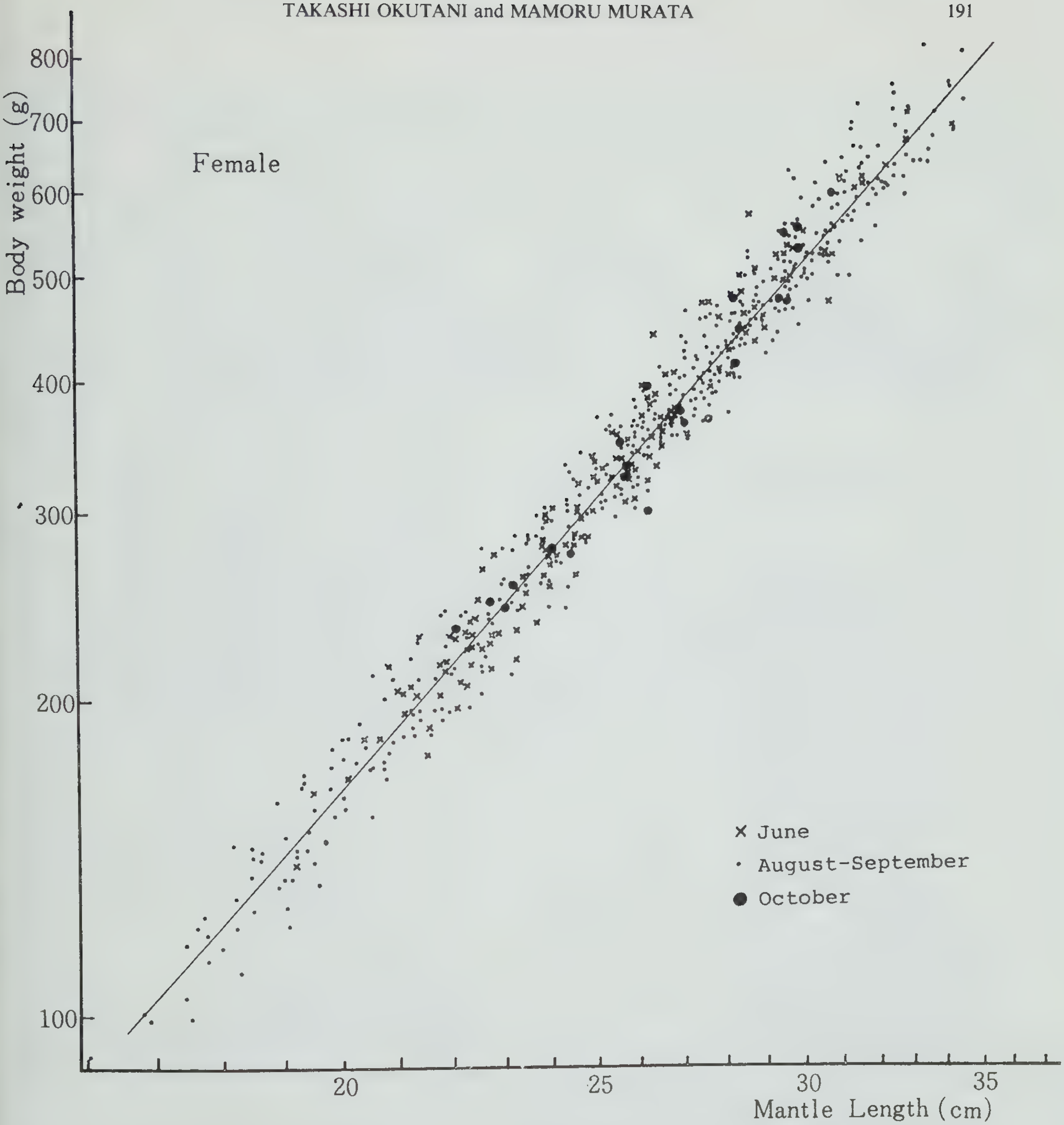

Figure 2. Relationship between mantle length and body weight (from Murata & Ishii, 1977).

schools seem to be distributed throughout the Subarctic water mass, males usually occupy half or slightly less than half of catch, but in August-September, when the fishing ground shifts westerly females are far more dominant than males (Naito *et al.*, 1977a).

3. *Distribution.* Young (1972) was the first to point out that *O. borealijaponica* replaced *O. banksi* in the cold waters of the North Pacific Ocean.

Distribution in time and space correlated with temperature preference of the *O. borealijaponica* population to the east of Hokkaido has been studied by Murakami (1975, 1976),

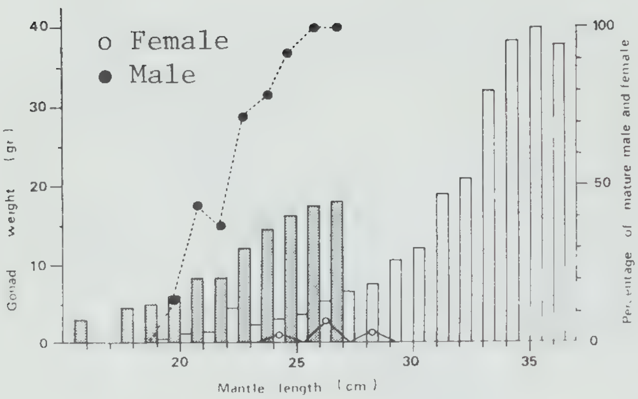

Figure 3. Mean gonad weight (blank bar: ovary; shaded: testis) and percentage of mature specimens by mantle length class of the 1976 catch (from Naito *et al.*, 1977).

Murata (1974), Murata *et al.*, (1976) and Naito *et al.* (1977a). According to these reports *O. borealijaponica* first appeared in this water as an incidental catch in salmon gill-nets in April. More substantial catches were taken by jigging in June in an extensive area from warm water to mixing and cold water areas north of 39°N up to 50°N. The temperature recorded for catches in this season ranged from 5°C to 20°C at the surface (Figures 4 & 5). As time passed the concentration of the school shifted northerly and by August-September was located along the polar front lying around 42°-45°N. The shift of aggregation (fishing ground) corresponded well to that of the 10°C-isotherm (Figure 6). In warm water years the squid migrated further north than usual but never penetrated into the Okhotsk or Bering Seas. Before disappearing from the fishing ground, the center of the distributon shifted to the coastal water mass and the southern rim of the Oyashio Branch. The whole scheme of seasonal distribution clearly demonstrates a northern migration for feeding and maturation and a southern migration for spawning.

Most of the studies cited above concerned not only this species but also other oceanic squids, such as *Ommastrephes bartrami*, *Todarodes pacificus*, *Gonatopsis borealis* and *Berryteuthis magister*. Differences in life histories, particularly migratory patterns and habitats, are reflected by differences in temperature preference. Murakami (1976) demonstrated that *O. bartrami* was fished in areas of high temperature (20°C or higher), *G. borealis* was jigged or tangled at much lower temperature (10°C or lower), while *O. borealijaponica* and *T. pacificus* were caught between 10°C and 15°C. The degree of distributional overlapping of these species varies by season in significant levels (Murata *et al.*, 1976).

4. *Food.* Not much information concerning the food of this squid is available. Some 90 to 100% of 4 samples (308 specimens) investigated by Naito *et al.* (1977b) had empty stomachs. The small amount of food identified consisted of small fishes and the same species of squid.

5. *Biomass.* The biomass of oceanic squids has not always been fully assessed over their vast distributional range. A trial stock assessment of *O. borealijaponica* was made by Murata *et al.* (1976) who drew the chart with contours of catch rate (number of squid caught per jigger per hour) based on the result of exploratory fishing by the Hokkaido Regional Fisheries Research Laboratory in the area west of 152°E and 40°-45°N since 1968. The population index P_i was obtained as $P_i = A_i \cdot \Phi_i$, where A_i is the number of $10' \times 10'$ grids and Φ_i, each contour level of abundance. The population index for the whole surveyed area was obtained by $P = \Sigma P_i$ and the density index by $\Phi = P/\Sigma A_i$ (Table 2). This value was applied to the equa-

TABLE 2

Population Index (P) and Density Index (Φ) of *O. borealijaponica* in the east of 150°E (After Murata *et al.*, 1976, and data of Hokkaido Regional Fisheries Research Laboratory).

Year	$P(\times 10^2)$	Φ
1968	8.9	3.23
1969	3.4	1.17
1972*	49.6	4.74
1973	7.2	0.67
1974	40.9	4.91
1975	28.5	4.12
1976	48.0	5.69
1978	6.7	0.51

* For June, otherwise for August-September.

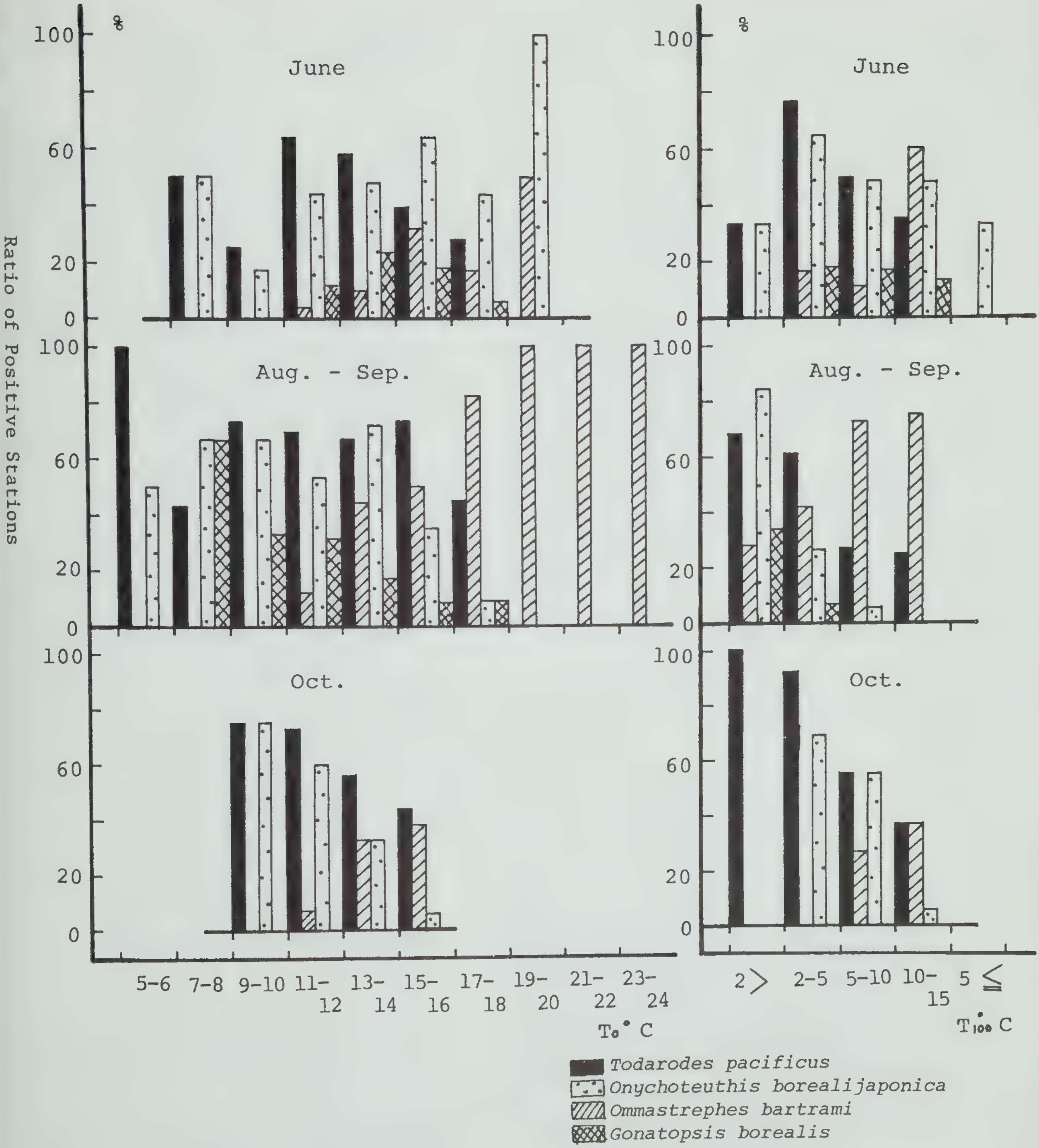

Figure 4. Relationship of positive jig stations to temperature at surface (T_0) and depth of 100 m (T_{100}) (from Murata *et al.*, 1976).

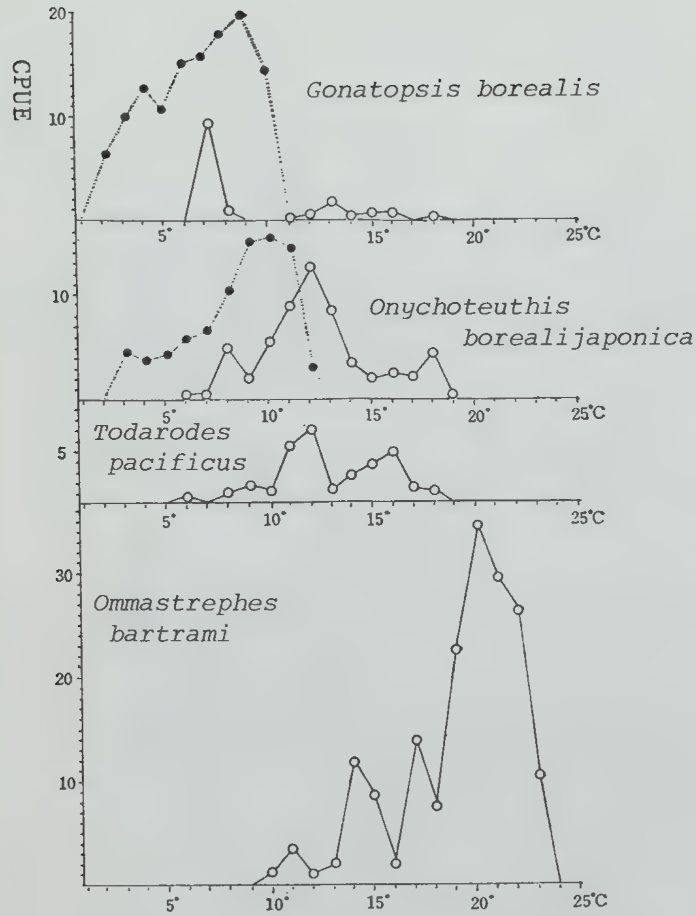

Figure 5. Relationship of CPUE (number of specimens per jigger per hour or per unit length of gill-net) to temperature by jigging (open circle: June-October) and by gill net (closed circle: April-July) (from Murakami, 1976).

tion, Catch ($\times$1 000 tons) $= 4.5 \times P$, obtained for *Todarodes pacificus*, in spite of the fact that consideration has not always been taken for species differences, variabilities of geographical coverage of survey by year, differences in species distribution patterns, vulnerability, etc. The result indicates that the potential catch of this squid species (mean $P=22.8$) could be 50 000 to 200 000 tons (Murata, in Okutani, 1977).

Acknowledgements

We wish to extend our thanks to Mr K. Murakami, Hakodate Fisheries Experimental Station, for his generosity in supplying us with data and illustrative materials.

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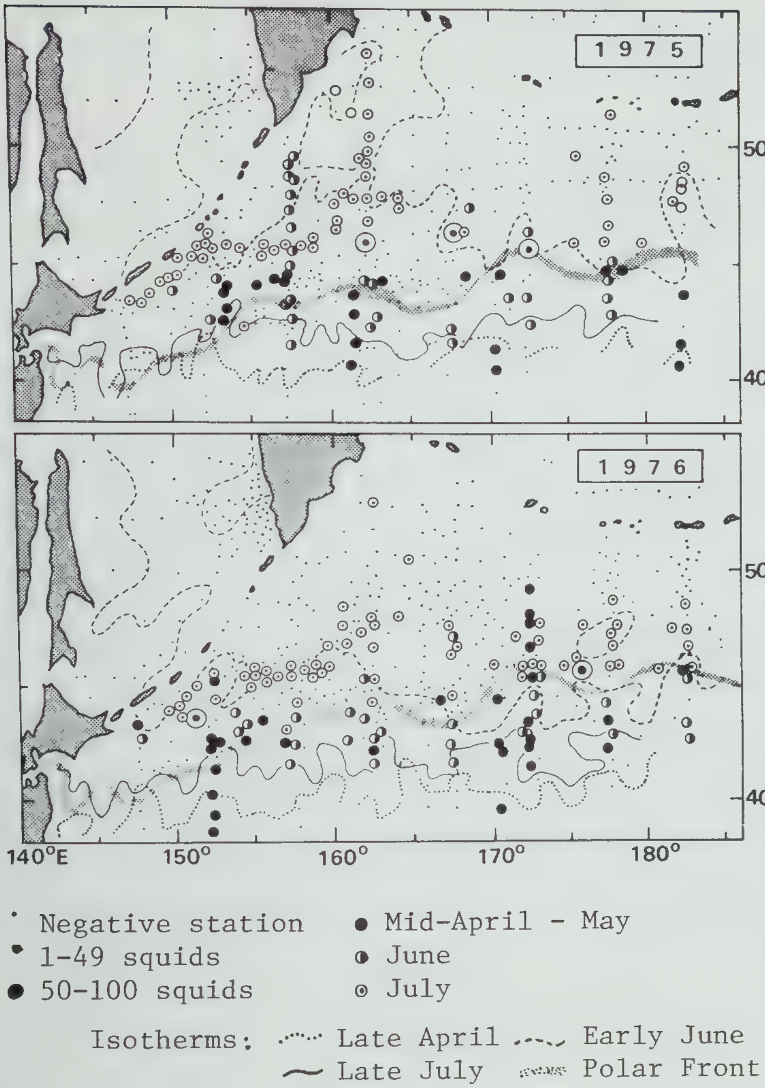

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DISTRIBUTION OF MESOPELAGIC CEPHALOPODS AROUND A WARM-CORE RING IN THE EAST AUSTRALIAN CURRENT

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Abstract

A warm-core ring of the East Australian current was sampled from August 1979 to May 1980 to investigate how its sustained thermal structure affected the distribution and abundance of micronekton, including cephalopods. Samples were collected at night with 1 hour tows of a midwater trawl (RMT 8) to a maximum depth of 540 m. The length, sex and maturity stage, together with temperature and depth of occurrence, were recorded for approximately 2000 specimens in 37 species of pelagic squid and octopus. The families Enoploteuthidae, Histioteuthidae and Cranchiidae contained most species and individuals.

The distribution pattern of species relative to water temperature, depth or geographical position relative to the ring was rarely consistent between different months of sampling. Multivariate analysis showed small-scale spatial and temporal homogeneity between the species composition of samples.

Distribution of some species did, however, indicate differentiation of regions relative to the ring. *Pterygioteuthis gemmata* was more abundant outside the ring whereas its congener, *P. giardi*, was more abundant at the edge of and outside the ring, in all months of sampling. Some species (e.g. *Spirula spirula*) occurred in a restricted range of temperatures and depths but abundances were too low for statistical analysis.

Large oceanic squid readily evade trawls and were not collected in the RMT samples. They were nevertheless of interest as predators in the pelagic ecosystem associated with the ring and, in particular, its encircling thermal front. Hand-held jig lines were used to collect these larger individuals, primarily of the species *Ommastrephes bartramii*. Their morphometry and stomach contents were studied in relation to the hydrography of the ring.

PROTEIN VARIATION IN *NOTOTODARUS GOULDI* FROM SOUTHEASTERN AUSTRALIA

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Twenty seven sample sets, each consisting of pieces of mantle muscle and digestive gland from 100 animals, were collected from a series of sampling stations in Bass Strait and off S.E. Tasmania and South Australia. A total of 30 different specific proteins were surveyed using standard cellulose acetate and starch gel electrophoretic techniques. Twelve digestive gland enzymes and two muscle enzymes showed inter-animal variability.

The phosphoglucomutase (PGM) variation in muscle had the appearance expected of a genetic polymorphism at this locus while the lactate dehydrogenase (LDH) variation could be so interpreted, though the patterns were different from those seen in vertebrates.

The variation observed in the digestive gland proteins was different from that described in any other group of organisms. Six or more band positions were found in the variable proteins and from one to six bands in all combinations were observed. The band strengths varied markedly and all band positions could be strong, weak or absent. There was no regular association of patterns in one enzyme with patterns in other enzymes. The genetic and/or environmental basis of this variation is unknown but clearly complex. Though the patterns observed varied widely from sample set to set, within any set only a limited number of the possible patterns were observed.

Further studies were restricted to the muscle LDH and PGM loci and to the variation in digestive gland, LDH, PGM and glutamate oxaloacetate transaminase (GOT). The effects of a range of environmental factors on these proteins was examined:

1. Organ heterogeneity

Five samples taken from different points along the length of the digestive gland of each of ten animals expressed similar phenotypes within each animal and the inter-animal variation could not be ascribed to the varying proportions of the various tissues found in different parts of this organ.

2. Sample deterioration

Ten animals were sampled on capture and resampled after 1, 2, and 4 hours at ambient temperature. There was no change in pattern. Samples retyped after extended periods of storage typed correctly.

3. Animal size, general condition (i.e. mantle thickness) and reproductive condition

There was no systematic effect of these variables on the patterns observed.

4. Food type

The ability of squid to transfer incompletely digested food to the digestive gland raises the possibility that the enzymes of the prey species were being typed as well as the squid proteins. However, analysis of protein patterns within schools by food type showed this was not so.

5. Feeding state

There were differences in the patterns observed between individuals with full and empty stomachs within a sample set. However, which electrophoretic patterns were related to which feeding state changed from set to set.

There was no systematic between-area variation in the frequencies of the muscle enzyme patterns.

The geographical distribution of the digestive gland variation in PGM and GOT was random while the LDH variation was nonrandomly distributed between areas. A series of sets from the eastern edge of the study area (namely, the set taken off Maria Is., a set from Flinders Is.

and sub-sets from Storm Bay and Lakes Entrance) consisted of squid with only a fast LDH pattern. Only 4 of these animals were found throughout the rest of the sets studied. The other bands observed for this enzyme occurred in all combinations throughout the region.

There was no evidence in this study of the presence of more than one *Nototodarus* species in the fishery. S. Collins (Personal Communication) was able to ascribe some of the sample sets studied to the proposed spring brood and others to the winter brood. There were no systematic differences between the observed electrophoretic patterns of these groups; however, the absence of a good series of allelic polymorphisms in the species made it difficult to obtain significant evidence on the number of stocks in the fishery.

RADIO-NUCLIDES AND HEAVY METALS IN *NOTOTODARUS GOULDI*

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Introduction

Cephalopods have been shown to accumulate heavy metals and some radio-nuclides to a remarkably high degree (Martin & Flegal, 1975; Heyraud & Cherry, 1979). The respiratory pigment in the blood of cephalopods is haemocyanin (Lontie & Witters, 1973) which in pure form has a copper content of 0.25% (2,500 ppm). The presence of high levels of copper is essential, but other heavy metals normally regarded as toxic are also present at high levels. The biological success of cephalopods indicates that they have an adequate mechanism for fixing the heavy metals in non-toxic form. Where dissections and analyses of different organs have been carried out, they show that the digestive gland contains the metals at much higher levels than those found in the white muscle (Martin & Flegal, 1975; Miramand & Guary, 1980). The radio-nuclide Po-210 follows the same pattern, with high concentrations in the digestive gland.

Po-210 is the major contributor to the natural radiation dose received by many marine organisms (Cherry & Shannon, 1974, Heyraud, 1982), and the squid digestive gland receives one of the highest recorded doses (Heyraud & Cherry, 1979). This makes Po-210 in squid of great potential value in food chain studies. Laboratory studies have shown that the cephalopod *Octopus vulgaris* can accumulate the transuranic elements Pu-237 and Am-241 preferentially in the branchial heart (Guary & Fowler, 1982).

Early knowledge of the levels and behaviour of potentially toxic elements is essential in the development of any fishery. This protects public health, and can prevent the problems that may be encountered with their later discovery.

Research Objectives

This preliminary work, involves the study of the distribution of heavy metals and the radio-nuclide Po-210 in cephalopods from the waters off south-east Australia. The work is concentrated on *Nototodarus gouldi* which is the common commercial squid species in this area. We are investigating the relationships between the elements being studied, and the sex, size and age of the squid. The work is being further extended to other species, including those found in Antarctic waters.

The programme will be extended to a study of the heavy metals and Po-210 in the food chain, in one direction to the predatory fishes and birds, and in the other direction to the zooplankton and phytoplankton. The sources of the large amount of copper needed by the cephalopods, and the capacity of the cephalopods to detoxify some elements usually regarded as highly toxic, will also be studied.

The behaviour of Po-210 is not well known, and is being investigated and compared with the metals. The presence of Po-210 in excess of that supported by its precursor Pb-210 indicates that it is accumulated independently of the Pb-210.

Methods

1. *Characterisation.* Squid were obtained in a trial fishery in Bass Strait and immediately snap frozen. The sex, weight and length of each animal was noted and the digestive gland removed. Tissues were freeze dried in preparation for analysis.

1. *Heavy metals.* A sample of the tissue (1 g) was digested under reflux in nitric-perchloric acid, and the trace metals determined by atomic absorption spectrometry or ICP atomic emission spectroscopy. An X-ray fluorescence analyser is being calibrated for the simultaneous determination of many elements in milligram samples of freeze dried tissue.

3. *Polonium-210.* A sample of the tissue digest was evaporated to near dryness and taken up in dilute hydrochloric acid. The Po-210 was plated out onto a silver disc, and

the alpha-activity counted (Flynn, 1968). Correction was made for radioactive decay since the time of sampling. The contribution of the Po-210 supported by Pb-210 was determined by re-plating and counting after a suitable delay (usually 3 months).

Results

Values from the literature for heavy metals and for Po-210 in the digestive gland of various cephalopods are summarised in Table 1, with preliminary results for *Nototodarus gouldi* from waters off south-east Australia.

Supported and unsupported Po-210 have been measured and at the time of capture about 0.3% of the Po-210 was supported by Pb-210. The level of Po-210 in the digestive gland of *Nototodarus gouldi* is higher than the levels reported for *Loligo* spp. and sufficiently high to make it useful for food chain studies.

The weight of digestive gland plotted against weight of the whole animal for *Nototodarus gouldi* collected on one night in Bass Strait is shown in Figure 1. The results indicate that there is high variability in both males and females.

Future Developments

The direction of future work depends on the results of experimental work in progress, and will include studies of the form of binding of the metals and radio-nuclides in the cephalopods, and the fate of these elements in the food chain. The main work will continue to concentrate on *Nototodarus gouldi*, but will be extended to other species, especially those of commercial importance in other parts of Australia.

Acknowledgements

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TABLE 1

Reported values for heavy metals and for Po-210 in the digestive gland of cephalopods. The concentration of Po-210 in seawater, given for comparison is 0.034 pCi/l. Results for *Nototodarus gouldi* are from the present work with the metals determined by L. Plues and the Po-210 by M. Heyraud. Other results are from Folsom & Beasley, 1973; Martin & Flegal, 1975; Heyraud & Cherry, 1979; and Miramand & Guary, 1980.

SPECIES	Ag	Cd	Cu	Fe	Zn
		(Metal concentration ug/g dry)			
Loligo opalescens	9.8-83	22- 265	680-15160	19-338	113- 892
Simplectoteuthis oualaniensis	14.0-40	427-1106	1520- 1940	260-415	162- 838
(Ommastrephes bartrami?)	4.4-39.6	71- 694	17- 696	149-850	93- 258
Octopus vulgaris	—	50 ± 10	2500 ± 700	700 ± 130	1450 ± 400
Nototodarus gouldi	2- 5	30- 100	50- 1100	340-820	470-1500

SPECIES	Po-210 (pCi/g dry)	
Loligo vulgaris	46-164	(Mediterranean)
Loligo vulgaris	49- 73	(Atlantic)
Loligo sp.	0.75	(N.E. Pacific)
Octopus vulgaris	23	(small)
Octopus vulgaris	22	(large)
Sepia officinalis	63	(small)
Sepia officinalis	54	(medium)
Sepia officinalis	44	(large)
Eledone aldrovandii	13	
Nototodarus gouldi	65-658	(Bass Strait)

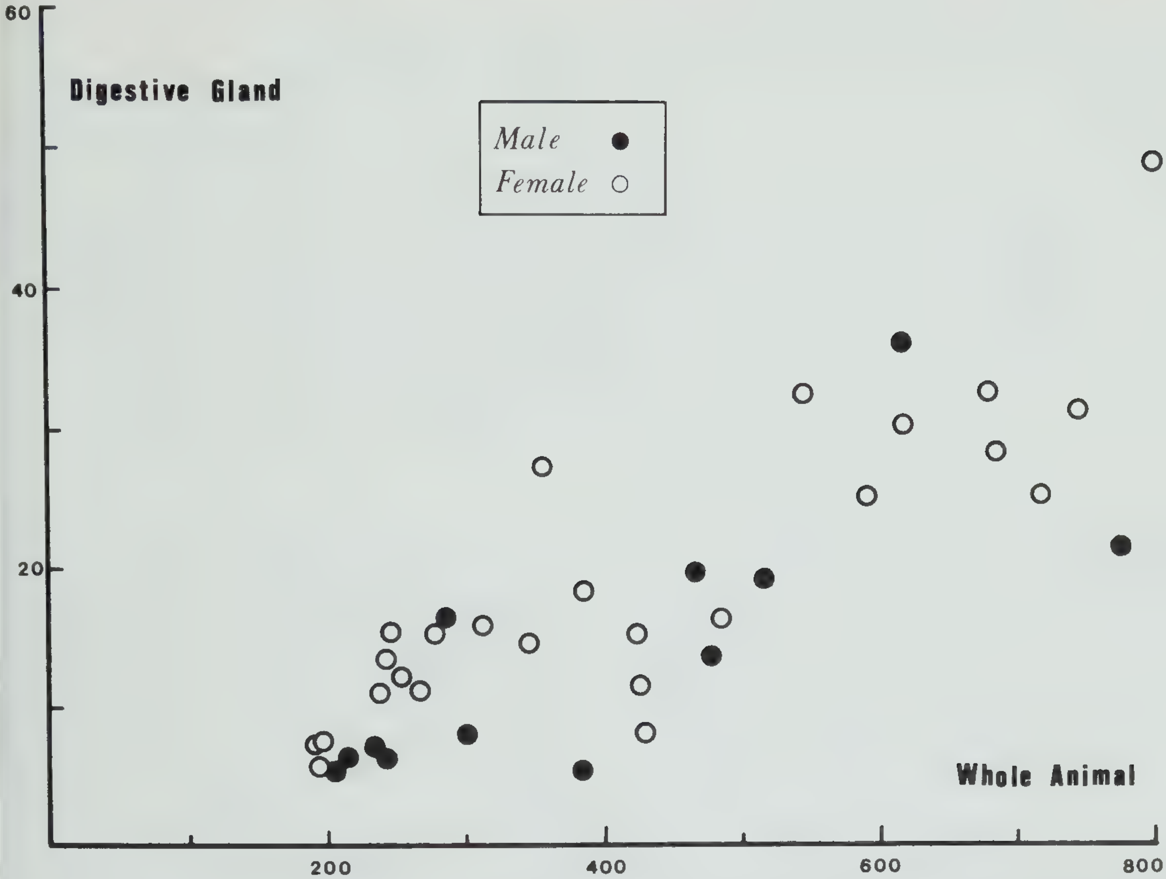

Figure 1. Weight of digestive gland *vs* weight of whole animal for *Nototodarus gouldi*. Figures are wet weight in grammes.

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LABORATORY OBSERVATIONS ON THE VISUAL ATTACK OF THE SQUID, *TODARODES PACIFICUS*

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Abstract

Observations on the visual attack of the squid, *Todarodes pacificus*, were made in concrete holding tanks. A 35 mm SLR camera with a motor drive recorded the squid visual attack. Using sardine fillet attached to a monofilament nylon or to the plastic body of a jig as bait, the attacks observed were fast and continuous which terminated with the squid grasping the bait with its arms. As observed also in other cephalopods (*Sepia, Illex* and loliginid squids) by other workers, prey capture using the arms instead of the tentacles were exhibited when the prey was stationary or slow moving. This similar behavior exhibited by *T. pacificus* may also be due to the slow introduction of bait into the tank. This behavior may be verified in actual squid fishing operations where the hauling speed of the jigging machine is reduced. Seizure of the jigs using the arms may lessen the chances of the hooked squid lost off the jig.

Introduction

Information on the visual attack of the squid may help in the design of the jigs. Murata (1978) reported a problem in jig fishing for the squid, *Ommastrephes bartrami* locally called "baka-ika" or "aka-ika". During rough weather, hooked squids are often lost off the jigs when brought out of the water. This may account for a considerable loss in the fishing operation. The cause of the loss of hooked *O. bartrami* was not clearly known. Both *Todarodes pacificus* and *O. bartrami* are ommastrephid squids and appear to have close ecological similarities. If their mode of life is not very different then their attack behavior also may be closely related. Information on the attack behavior of *T. pacificus* may thus be used to help understand the problem with fishing for *O. bartrami.*

Observation on locomotion on a closely related squid, *Illex illecebrosus illecebrosus*, were made by Bradbury and Aldrich (1969). Working with confined squid they analyzed general locomotions such as "lift-off", hovering, free swimming and turning. Williamson (1965) also made general observations on *I. illecebrosus* in Newfoundland waters. His work analyzed swimming, reconnaisance and attack, color and behavior of the squid after capture. Messenger (1977) reported details of the attack or "prey capture" in the cuttlefish *Sepia*. Messenger divided the attack into three phases: (1) *attention*, turning of the body axis towards the prey which may be accompanied by changes in body coloration, (2) *positioning*, an approach towards the prey till it is at attacking distance where it pauses for up to 10 seconds, and (3) *strike*, the whole animal lunges forward slightly and the tentacles are ejected at high speed to seize or capture the prey. Kier (1982) described the attack behavior of *Loligo pealei* and *L. plei* in the laboratory in his study of the musculature of squid arms and tentacles. He divided the attack pattern into three phases as employed by Messenger (1977).

First hand information on squid attack behavior in the natural environment and the results on aquarium studies by other workers will be referred to for comparison with observation presented here on *T. pacificus.*

Materials and Methods

General observations on the attack behavior of *T. pacifica* were taken from squids in concrete holding tanks of the Hokkaido Hakodate Fisheries Experimental Station, Hakodate, Japan, while the author was developing maintenance technique for squid in laboratory confinement (Flores, *et al.*, 1976, 1977). Detailed observations were made in summer of 1978 using squids in the holding tanks which were later used in the simultaneous discrimination tests for light intensity and color (Flores, 1983).

Feeding of squid in confinement allowed repeated observations on its visual attack on the bait introduced. The squids were maintained in concrete tanks (230 cm $\times$ 180 cm $\times$ 120 cm) and

fed daily with sardine fillets. With this size of tank, the bait when introduced can be seen from all parts of the tank.

The squid visual attacks were recorded using a 35 mm SLR camera with a motor drive where the maximum film advance was at five frames per second. Using this method, a rough estimate of the squid attack speed can be calculated. Daily observations were noted during feedings and are included here in describing the attack behavior of *T. pacificus*.

Results

General swimming behavior. Healthy squids maintained in laboratory confinement when not disturbed swam quietly back and forth or moved from one side of the tank to the other without hitting the walls. Most animals spent considerable time just hovering or suspended at mid-water depth with little forward and backward movements. The arms and tentacles were "relaxed" and drawn together, but not tightly (Figure 1). The fins beat with a short vertical motion and at times a horizontal component was also present which took the form of a wave moving headward at the periphery of the fins.

Strong dorso-ventral beating of the fins together with jet propulsion were observed when a squid moved away from a disturbance such as the quick introduction of a scoop net into the tank or the sight of an attacking squid. When the disturbance was great, the escape was in most cases accompanied by a release of ink. During the escape, which was fin first, the arms and tentacles were drawn tightly together to form a cone. This was presumably to reduce the drag force.

Weak squids either constantly hit the plastic sheet bumper lining the walls of the holding tank or settled to the bottom. These behaviors were discussed in detail in previous papers (Flores *et al.*, 1976, 1977).

Feeding. The squids described in Flores *et al.* (1976) that were subjected to a 10-day survival test without feeding immediately began to feed on sardine fillets when first introduced on the 11th day. Attacks were fast and the detailed movement could not be resolved by the unaided eye. The same fast attacks were also observed when the plastic body of a squid jig was introduced. Squids with empty stomachs seized any object smaller than itself when presented.

Squids used for behavioral studies (Flores *et al.*, 1978, Flores 1983) were fed with sardine fillets on the second day after being transported from the fishing boats to the holding tanks in the laboratory. The same fast attacks were also observed for these squids.

Analysis of the visual attack. The fast and continuous attack was the most commonly

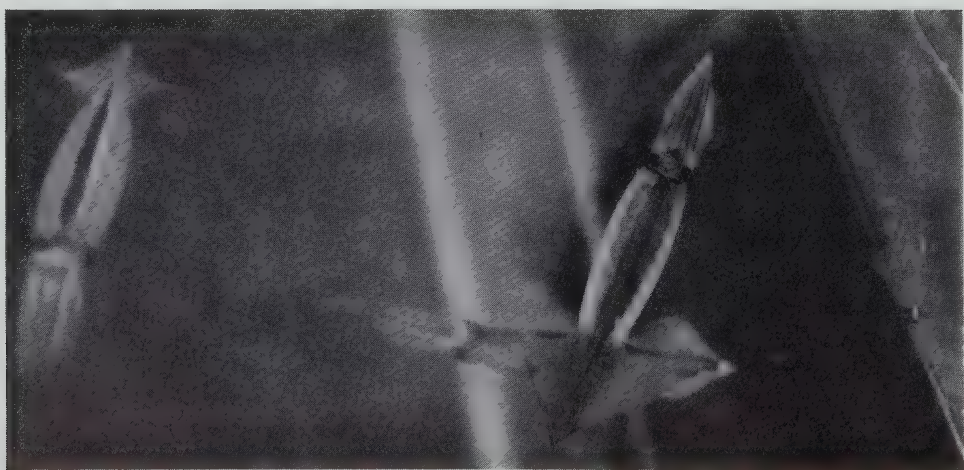


Figure 1. Squid, *Todarodes pacificus*, after six days in confinement shown undisturbed.

observed attack behavior. The components of this attack was (1) attention, (2) approach and (3) seizure. Attention was shown when the squid turned towards the direction of the bait. The yawning plane was horizontal when the squid was at the same level with the bait. When the bait was either above or below the swimming level of the squid, horizontal and vertical components were observed. In most cases, attention was accompanied by a display of dark body coloration and the arms and tentacles were drawn tightly together to form a cone. In this posture, binocular vision was attained when the eyes converged towards the body axis.

The approach started when the squid swam head first towards the bait. Figure 2, frame A shows the squid at the end of its approach to a bait attached to the lower portion of the plastic body of a squid jig. The arms and tentacles are still drawn tightly with the eyes directed towards the bait. During a tail first approach, a squid usually swam obliquely towards the bait, passed it by about 40 cm and then went back head first for the seizure.

Seizure started when the tentacles were spread laterally (Figure 2, frame B). The distance between the bait and the tip of tentacles at this moment varied. In this Figure, the tentacles with suckers exposed were extended laterally without touching the bait while the arms were opened (frames C and D) for the seizure. The tentacles appeared to cover the lateral escape of the bait as they would probably do in nature with a live bait. The bait was then seized using the arms and brought to the oral region. Once the bait was secured by the arms the tentacles were relaxed but not retracted (see also Figure 3 frame B and 4 frame D). Seizure took about 0.8 to 1.2 sec depending on the distance between the squid and bait at the start of seizure. In Figure 2 the mantle length of the squid is about 20 cm. The attack speed calculated here at frame interval of 0.2 sec, would be roughly 50 cm/sec.

When the bait was secured in the oral region, the squid started to retreat with strong dorsoventral beating of the fins (see Figure 5, frames F to J). In most cases the dark body coloration

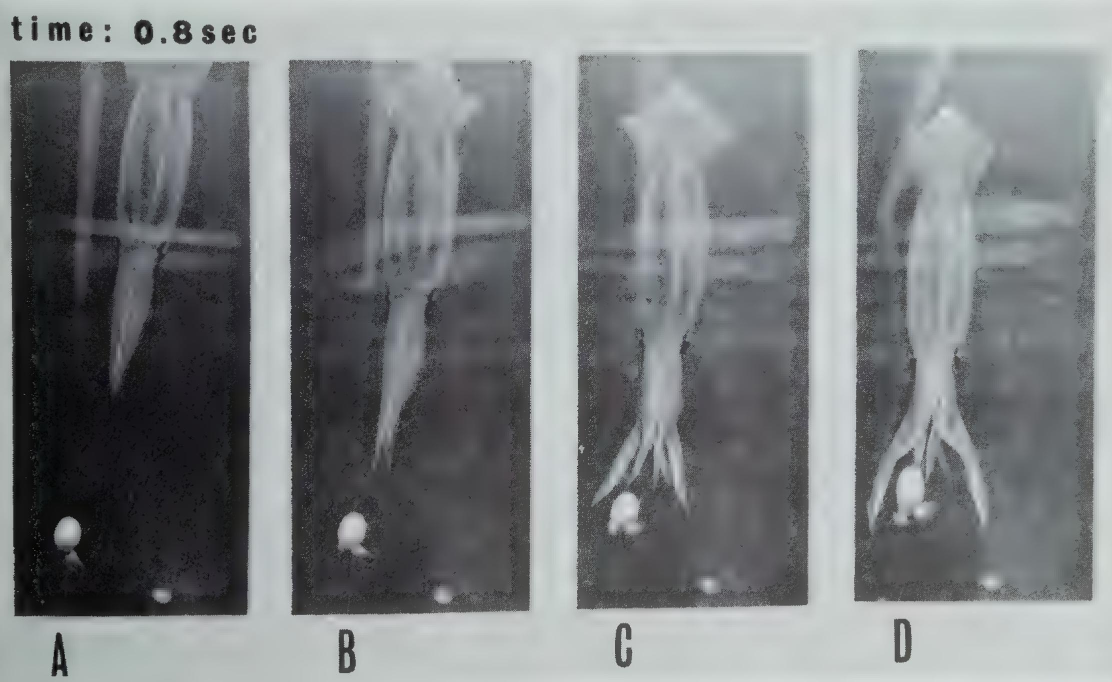


Figure 2. Squid attacking a bait attached to jig. A sequence of postures clearly showing binocular vision.

disappeared leaving only a dark streak extending from mid-dorsal to the tip of the fins. Using the film advance speed of the motor drive as reference, a squid attack took about 3 to 4 sec depending on the distance of the squid from the bait at start of approach and at start of seizure.

Although the majority of attacks fit the fast and continuous description some showed slight variation. An example of one variation is shown in Figure 3 where the arms were spread wide open in all directions like an open umbrella. In this type of seizure, the bait passed the arms and hit the oral region before the arms closed. This probably represents a case where the distance to the bait was not clear to the squid. Again, in this type of seizure, the tentacles were not used.

Figure 4 shows part of a sequence of attack postures similar to Figure 2 except for the start of seizure (frame B) which was very close to the bait. The variations in distance of squid to bait at start of seizure suggests that the determination of distance was approximated within a given range. No seizure started at a distance of about more than 20 cm from the bait, and no bait was observed hit by the arms and tentacles still in the form of a cone. Even in this situation where seizure started very close to the bait, the tentacles were not used.

A sequence of postures in Figure 5 shows clearly the eyes of the squid directed to the bait maintaining binocular vision at seizure (frames A to E). With the bait secured by the arms, the squid shift back to monocular vision (the eyes at laterally directed position) while starting to retreat with strong dorso-ventral beating of the fins (frames F to J). In this Figure, the squid seized first the body of the jig with its arms and then the lower end of the jig where the bait was attached was turned towards the oral region (frames H, I, J). The body of the jig was held close after contact and then tightly which may be due to the presence of the natural bait at the lower end of the jig.

Figure 6 shows two squids attacking the same bait from one direction. The presence of a second squid attacking the same bait did not disturb the attack pattern. Other similar attacks would be two squids approaching the same bait at right angles to each other. The attack pattern could be disrupted while a squid was still approaching the bait, but once the seizure phase began, even if the bait was moved, the direction of attack continued unchanged.

There were cases in the holding tanks where a squid would make a sudden stop or a pause as it approached a bait. In rare cases a squid would make a full stop in the middle of a fast ap-

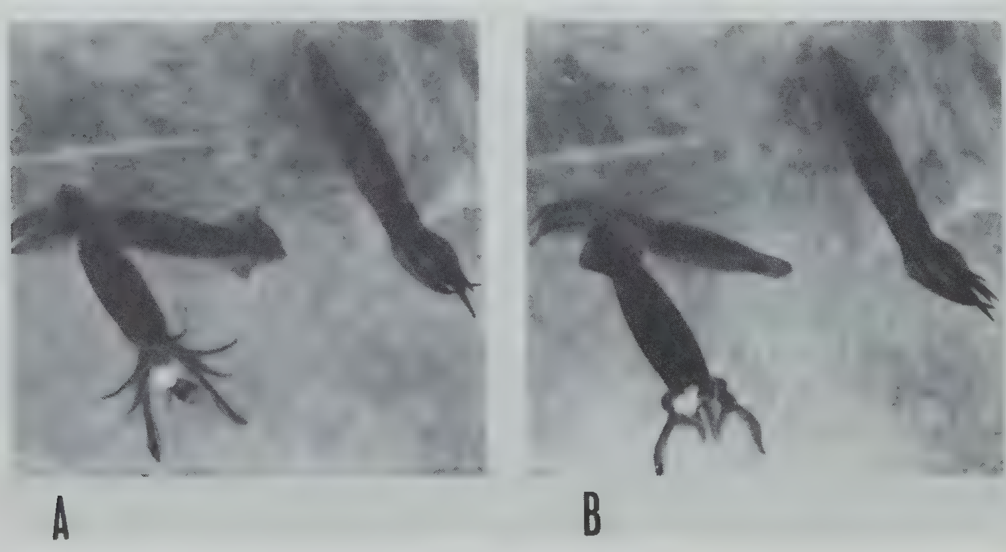


Figure 3. A fast and continuous attack with arms spread out in all directions at seizure.

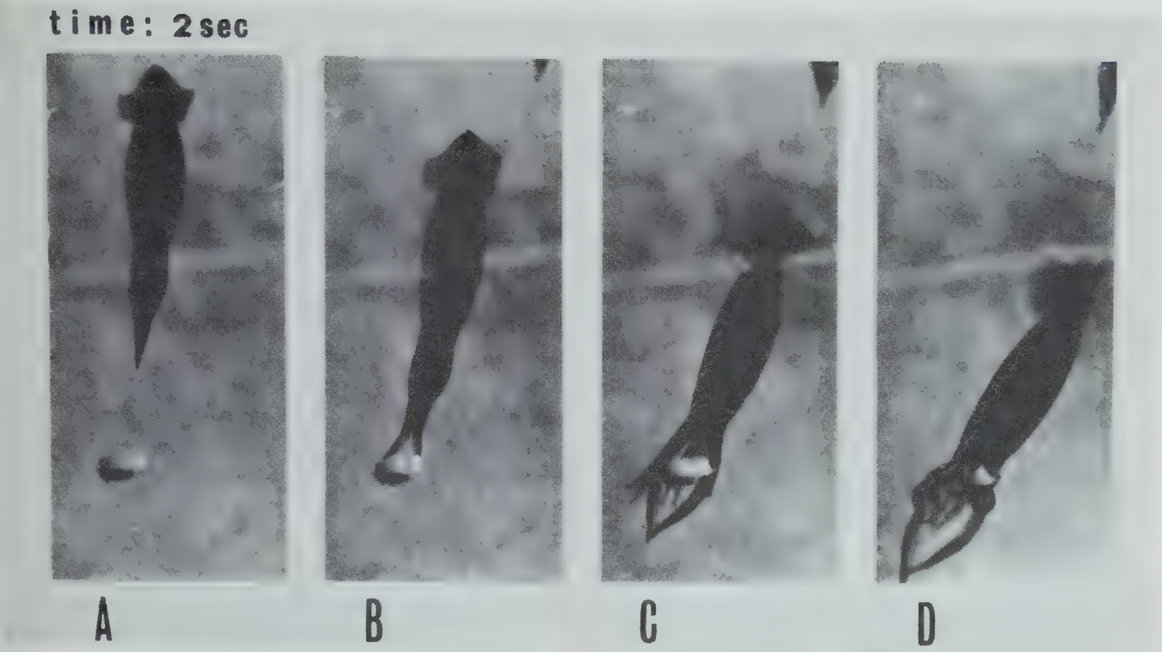


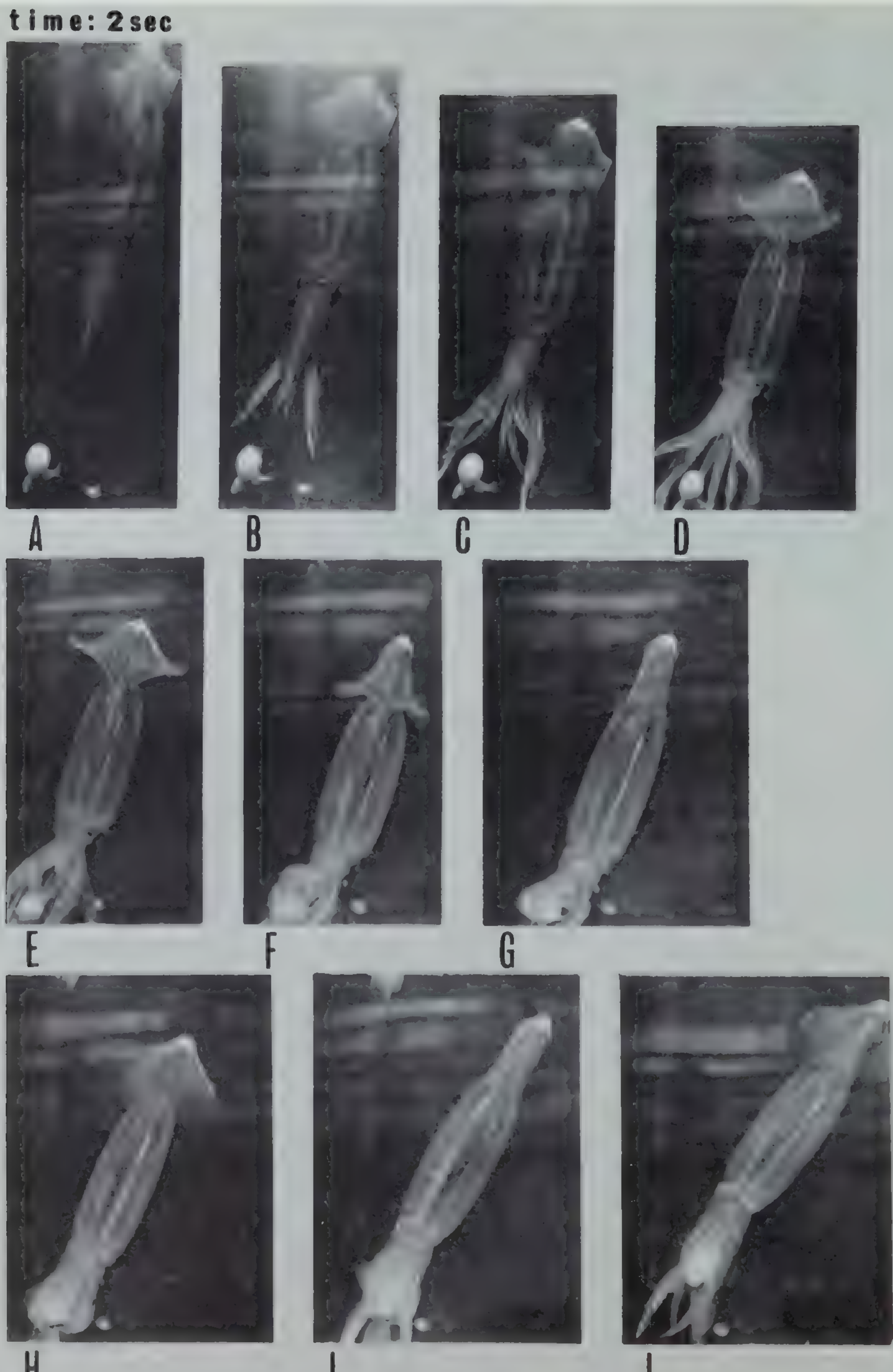
Figure 4. A fast and continuous attack with tentacles starting to spread at bait position, Frame B.

proach by spreading all its arms wide open. It was not known what caused these abrupt reactions which occurred at about 40 cm from the bait. More frequently, when a new form of bait was introduced for the first time, a squid would pause during a slow approach. This movement was stopped by the action of the fins and not the arms, though it may have been aided by the funnel which was not visible from above.

Discussion

The general swimming behavior observed here was the same as those described by Williamson (1965) for *Illex*. Williamson observed multiple squid attacking a jig at the same time and also a case where the squid approached the jig tail first and then turned to seize the jig after passing it. He called this type of approach a "reconnaissance". The approach component of attack was called "positioning" by Messenger (1968) since his *Sepia* always paused at a distance less than its mantle length away from the bait before seizure. In the case of *T. pacificus* where most attacks were made without a pause before seizure this component is best termed as "approach". Similar observation was reported by Kier (1982) for loliginid squid where also the pause before seizure was not exhibited. The approach continued up to the point of tentacle ejection.

Messenger (1968) reported that *Sepia* used its arms when catching slow moving crabs. However, in order to catch live prawn, the tentacles were used by projecting them rapidly forward ahead of the arms. Kier (1982) described this final phase of the attack for loliginid squid as when the tips of the tentacles are approximately 4 to 6 cm from the prey, the squid lunges towards the prey, the arms are flared out from the previous cone, and the tentacles are extended rapidly. However, Kier further stated that when the prey is stationary, the tentacles are sometimes not used and the squid simply lunge forward and grasp the prey with their arms. Bradbury and Aldrich (1969) in maintaining *Illex illecebrosus* reported the same behavior when feeding the squid with dead fish (*Mallotus villosus*) suspended by means of a monofilament nylon line. Similar observations were made here for *T. pacificus* where the slow sinking sardine fillets were used as baits. The plastic body of the jig with a sardine fillet attached at its lower portion (Figures 2 & 5) was presented with slow up and down movement.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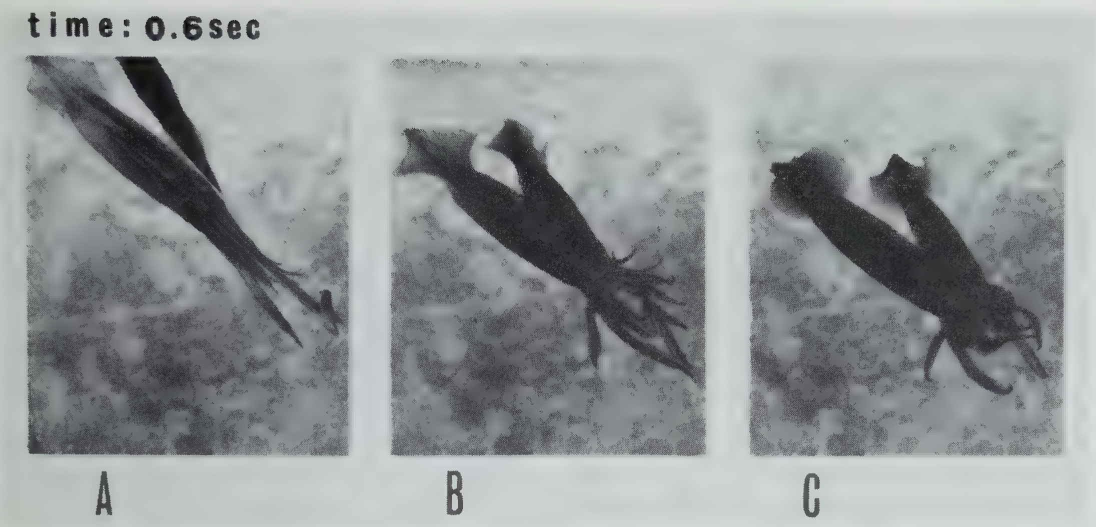

Figure 6. Two squid attacking the same bait from the same direction.

Out of the 175 squid observed in the present study, only one was observed to seize the sardine fillet with its tentacles. In this case, the tentacles were ejected at about the time the tentacles were spread laterally just prior to seizure. As in *Sepia*, the tentacles were ejected together and parallel. The suckers on the tentacle clubs seized the bait which was then brought to the oral region.

Seizure of the jigs using the arms may lessen the chances of the hooked squid lost off the jig. Four pairs of arms produce a better hold than a pair of tentacles. From the findings in this present study, arm seizure is exhibited when the bait or prey is slow moving. This behavior may be verified in actual fishing operations where the hauling speed of the jigging machine is reduced.

Acknowledgement

I thank Dr S. Igarashi and T. Mikami of the Faculty of Fisheries, Hokkaido University for their encouragement and assistance. I also thank the Director and Staff of the Hokkaido Hakodate Fisheries Experimental Station for the facilities. I am most grateful to Drs C. Roper and R. Hanlon for their valuable suggestion and criticism. This work was supported in part by a Japanese Ministry of Education Scholarship.

Figure 5. Squid attacking a bait attached to jig. A sequence of postures showing binocular vision at seizure (Frames A to E) and shifting to monocular vision at retreat (Frames F to J).

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VISUAL DISCRIMINATION TESTING IN THE SQUID *TODARODES PACIFICUS*: EXPERIMENTAL EVIDENCE FOR LACK OF COLOR VISION

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Abstract

Squids were taught by a reward and punishment paradigm to visually discriminate between lights of various intensities and colors using the simultaneous discrimination tests. The learning ability of the squid was established when it made discrimination between screens presented with lights of different intensities. For color discrimination test, the squid did not discriminate a green light (523.5 nm) from a blue light (450 nm) projected on separate screens.

The results of the present study which agrees with previous behavioral findings strongly suggest that *Todarodes pacificus* is color blind. With regards to squid fishing, the use of colored underwater lights does not seem practical in view of the findings in this study.

Introduction

In this study, squids were taught by a reward and punishment paradigm to visually discriminate between lights of various colors and intensities. The objective of the testing was to determine if *Todarodes pacificus* demonstrated a preference for squid jigs of specific colors, with the ultimate goal of designing a more attractive and efficient jig for commercial fisheries.

In squid fishing, a variety of small underwater lights of various intensities and colors are used for the attraction of squid to jigs. Recently, underwater chemical lights have been introduced in squid jig fishing. All these lights are used without any knowledge of the squid vision. The present study provides some information on the vision of the squid, *T. pacifica*, with regards to the color and intensity of light which could be applied to fishing. Also, this study provides information on the learning ability of the squid which is valuable for comparative study on animal behavior.

Among the cephalopods, the octopus has been widely used for learning experiments ranging from visual discrimination of orientation and form (Sutherland, 1957, 1960, 1960a, 1963; Sutherland & Muntz, 1959; Messenger & Sander, 1971) to monocular discrimination (Messenger & Sander, 1972), and visual preference (Messenger *et al.*, 1973). This area of study has been concentrated on the octopus because it is available and easy to maintain under laboratory conditions. During experimentation, the octopus can also withstand extensive manipulation or handling.

With regards to the hue discrimination using shapes painted red, green or blue, Messenger *et al.* (1973) presented evidence that strongly suggests that the octopus (*O. vulgaris*) lacks color vision. Roffe (1975) using colored lights reflected on a white disc also produced the same results. Again, Messenger (1977b) using colored shapes presented simultaneously showed further evidence that *Octopus* is color blind. Based on the above information and the similarity of eye construction in cephalopods it is likely that all cephalopods do not possess color vision. However, because of the wide ecological diversity within the class ranging from bottom dwellers to migratory pelagic species, a generalization on the absence of color vision may not be acceptable.

Outside of the octopus few other cephalopods have been used for learning experiments. Only recently have simple experiments of this sort been applied to *Sepia* (Messenger, 1977a). Messenger was able to train the cuttlefish not to attack a prawn inside a tube. After repeated unsuccessful attacks, the number of strikes decreased rapidly until the cuttlefish completely stopped attacking the prawn when it was presented.

Until now, no learning experiments have been performed on squid principally because laboratory handling and maintenance is difficult. Behavioral studies on squid in laboratory conditions started when Flores *et al.* (1976, 1977) developed an efficient handling and maintenance technique for *T. pacifica*. Flores *et al.* (1978) determined the absence of

color vision by using colored objects (stripes) as shapes in discrimination by optomotor response. The disadvantage of this method was that there was no control over the brightness of the objects presented, and that the brightness differences between objects induced some amount of optomotor response. Here, the discrimination by learning with the use of colored lights allowed the observer to control brightness.

Materials and Methods

Experimental animals. The water off Hakodate, Japan, is a major fishing ground for the Japanese common squid, *Todarodes pacificus.* Over-night fishing operations were conducted in this fishing ground by 5 gross ton squid jigging vessels. These vessels were fitted with live hatches at midship. The automatic jigging machines mounted on the bulwark had slipways connecting them to the openings of the live hatches. Jigged squid would fall on to the slipway then into the live hatches.

The squid used in this study were taken from these vessels at the fish landings and transported to the Hakodate Fisheries Experimental Station in aerated 50 litre plastic pails. The handling and maintenance of squid are as described in Flores *et al.* (1976).

Experimental tanks. The wet laboratory of the Hakodate Fisheries Experimental Station had a row of five concrete tanks of identical size (230 cm × 180 cm × 120 cm). In two tanks the walls and bottom were black while the other three were white. The two black tanks were used in this study while the other tanks were used as holding tanks for other studies. One black tank was used to receive and hold newly caught squid while the other tank was used as test tank for discrimination experiment.

Simultaneous discrimination test. This was conducted in October, 1978. Ten newly caught squid were secured from a squid jigging vessel at about six in the morning and transported to the laboratory where a black holding tank was made ready to receive them. The other black tank was set up for the simultaneous discrimination test (Figure 1).

In the holding tank, squid were trained to feed on sardine fillets (bait attached to a line) for eight days. Feeding was done regularly at night with the tank lighted by a 40W fluorescent lamp overhead. The behavior of the squid during feeding was closely observed in order to choose the squid that would be best suited for the test.

When the squid were regularly feeding on 2 g sardine fillet, two squid, that were good feeders and had fins with the least injury, were transferred to the adjacent test tank with the simultaneous discrimination apparatus installed as shown in Figure 2. The two squid tested were easily distinguishable because of a slight difference in size, and were marked as (A) for the better squid (♀, ML 21.5 cm) and (B) for the smaller one (♀, ML 20 cm).

In the test tank an overhead 20W fluorescent lamp covered with a translucent white plastic plate (1 mm thick) was provided in order for the observer to see the squid. A curtain of thick black cloth was hung above the side of this tank as shown in Figure 1 to prevent the penetration of bright light coming from the other tanks which were lighted with a bare 40W overhead fluorescent lamp. Another curtain made of black plastic sheet was hung in front of the simultaneous discrimination apparatus to minimize disturbance from movement of the observer.

Figure 3 shows the light projection set designated for this experiment. The light source was a halogen projector lamp (21V, 150W) commercially used for 8 mm cinema projector. Interference filters in the light path produced the desired color or hue. The intensity of each light was controlled by using neutral density filters (Wratten gelatin filter) at 0.5 log-unit steps. The light was then reflected off two front surface mirrors, down a black duct into the water, to a 10 cm square frosted glass which served as a screen. On the outside the glass was covered with a black adhesive plastic sheet with a 6 cm diameter hole cut out at the centre. This produced a circular 6 cm diameter screen appearing underwater. This circular screen serves as the "shape" which could be designated as a negative screen (−) or a positive screen (+) depending on the intensity or color of light displayed. An air bubble outlet was mounted at

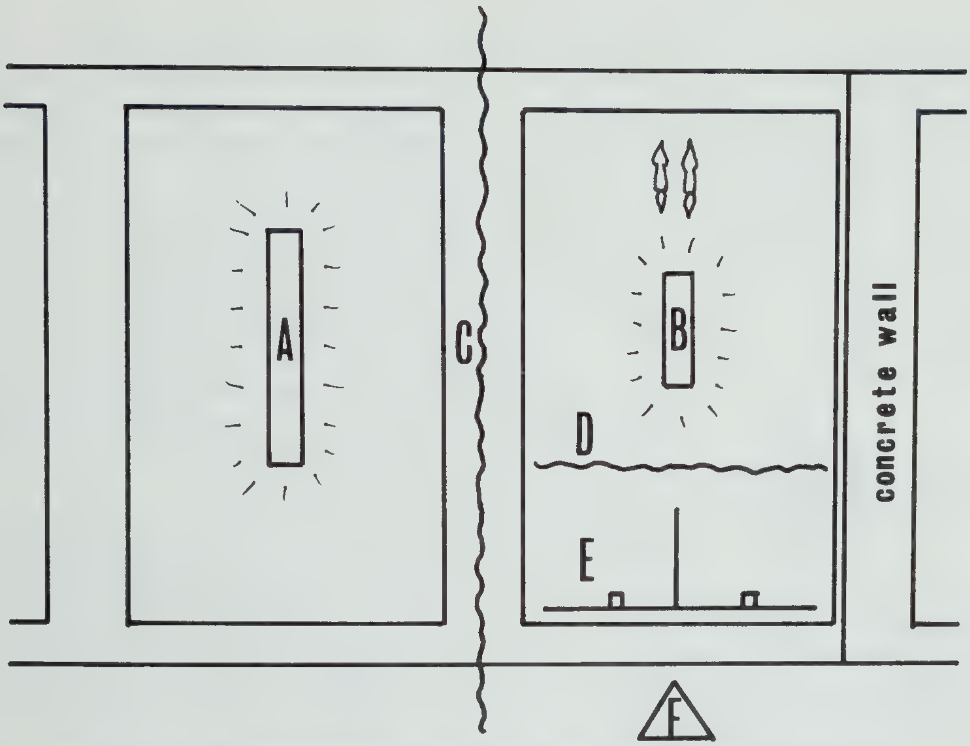

Figure 1. Floor plan showing experimental tanks used for simultaneous discrimination test (SDT); (A) 40w fluorescent lamp over holding tank, (B) 20w fluorescent lamp over experimental tank, (C) curtain, black cloth, (D) curtain, black plastic sheet, (E) SDT apparatus, (F) observer.

the lower corner of the duct with a plastic tubing connected to an ordinary aquarium air pump. The air bubbles when released serve as a form of punishment for an approach on the screen designated as negative screen.

The pair of light projection sets was connected to a switch box coupled with a voltmeter. The power source from an AC 100V outlet was led to a variable transformer before being connected to the switch box. This arrangement produced the same amount of electricity going to each light projection set.

Narrow band interference filters, green (523.5 nm) and blue (450 nm) were selected for this study in accordance with the spectral sensitivity curve for *T. pacificus* obtained by colorimetric method (equal energy spectrum) as reported by Orlov and Byzov (1962). The spectral sensitivity curve shows that at these wavelengths, the squid retina is equally sensitive, and so these colors should appear equally bright to the squid. Since the spectral sensitivity of the squid is high at the blue and green part of the spectrum, it should be easy for the squid to see these colors. The detailed characteristic of the interference filters used are shown in Table 1.

Table 1

Characteristics of interference filters based on data furnished by manufacturer (Vacuum Optics Corp., Japan).

	Green	Blue
Transmission maximum (nm)	523.5	450
Half-band width (nm)	13	20
Transmissivity maximum	45	41.3

The pair of light projection sets was mounted on a platform fixed at the upper edge of the deep wall of the test tank as shown in Figure 2. To this platform was also fixed a large piece of black painted marine plywood that fits down into the tank serving as a uniform background

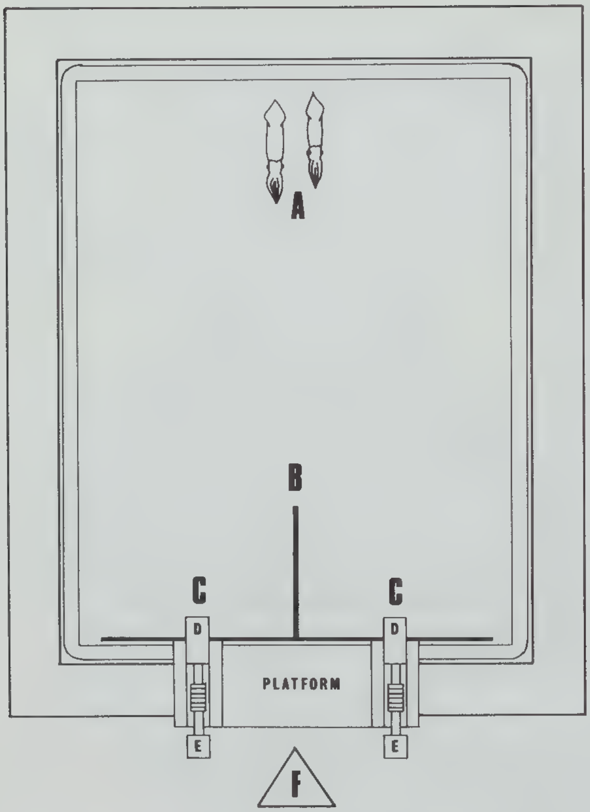

Figure 2. Overhead view of simultaneous discrimination test tank; (A) squid start position area, (B) partition, (C) feeding area, (D) screen, (E) halogen lamp, 21v, 150w, (F) observer.

of the circular screens underwater. At the centre of this background, a partition was fixed running lengthways down the tank. The length of the partition was 50 cm. This partition separated the left screen from the right screen so that when the squid was at one side the other side was not visible.

Experimental procedure

Pretraining 1. Upon transfer to the test tank the two squid were trained to feed on bait (sardine fillets) attached to monofilament nylon line (0.2 mm dia.) and hung in the feeding area (Figure 2, C). The feeding was done at night with white light projected on the circular screen. Bait was lowered in each feeding area simultaneously and presented for about one minute with slight up and down movement. The bait together with the white light would appear as shown in Figure 4a. Between trials a three-minute interval was allowed. The white light projected on the circular screen was kept on during the three-minute interval. For reference, the underwater illuminations of the screen with its light source masked with neutral density filters at 0.5, 1.0, and 1.5 log-units were 80, 20, and 3 lux respectively. The measurements were done using a Cds light sensor fixed 15 cm away from the screen. A minimum of 10 trials and a maximum of 20 trials were made for each session. During each test day one session is run at night.

Pretraining 2. Since no previous study has tested squid visual discrimination, the following experimental procedures were tried on the first day to determine if such procedures were suitable for this species.

Method 1. The circular screen was presented together with the bait as in Pretraining 1. The squid was allowed to seize the bait at the circular screen with white light projected (positive screen, +) at the same intensity as in Pretraining 1.
The other screen was also presented but without light (negative screen, (−) as shown in Figure 4b. For this screen, the squid was not allowed to seize the bait. Instead punishment was administered in a form of air bubbles.
The screens were exposed throughout the session and a trial begun by introducing bait into the feeding area of each screen as in Pretraining 1. A minimum of 10 trials were made for each session.

Method 2. Each trial started with the presentation of the screen by slowly pulling up the black plastic plate (11×11 cm) hung in front of the screen. Both screens were presented simultaneously and were exposed for one minute as shown in Figure 4b. After each trial, the black plastic plates were lowered to cover the screen. A three-minute interval was allowed between trials. A minimum of 10 trials were made for each session.

An approach means a squid goes toward the screen and when it was about 10 cm away from the screen, bait was presented as a reward when the approach was made to the lighted screen (positive screen, +). When approach was made on the unlighted screen (negative screen, −), air bubbles were released as punishment.

For both methods, a trial only started when the squid were in the starting area as shown in Figure 2. At this position, both screens were equally visible. The positions of the screens were varied from side to side in a semi-random sequence (Roffe, 1975) to prevent position fixation.

Method 2 was adopted for the rest of Pretraining 2 and for discrimination test using light of various intensities and colors. When using the white light, the power supply was set at 10V. It was feared that bright light might prevent the squid from approaching the screen. For the colored lights, the power supply was at 15V.

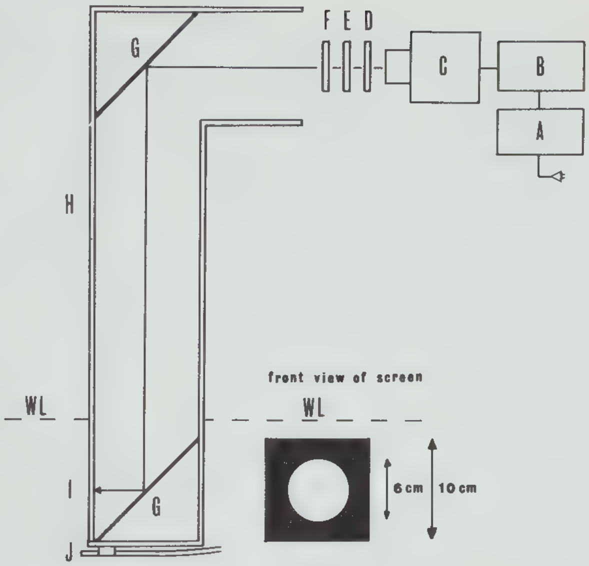

Figure 3. Light Projection Set; (A) variable transformer, (B) switch box and voltmeter, (C) light source, (D) heat filter, (E) neutral density filter (NDF), (F) interference filter (IF), (G) front surface mirror, (H) duct, (I) frosted glass screen, (J) air bubble outlet, (WL) water level.

Results

Simultaneous discrimination test. (SDT)

Pretraining 1. Training was started on the third day after transfer of squid into the test tank. The daily performance of each squid is shown in Table 2. Training was continued until a squid took ten pieces of bait during one session. This was necessary because the following discrimination test required a minimum of 10 trials per session, and for each trial bait was presented as a reward for an approach to the positive stimulus. On the 4th day, squid B took ten pieces of bait for one session while squid A made no approaches to the lighted screen.

A high percentage of successful trials can be attained from a squid that is able to consume ten pieces of bait or more per session. In the holding tank, squid stopped responding to bait presented after consuming enough amount of food. A squid, satisfied with say three pieces of bait, will most likely not respond to more trials.

The low percentage of successful trials will result in slow learning on the part of the squid. During this training, squid A did not perform well, but it was hoped that this squid would catch up during the following experiments.

Pretraining 2. Day one of training was devoted to the testing of Methods 1 and 2. Method 1 was not suitable because simultaneous presentation of bait produced problems of equal stimulation. Since baits attached to lines were presented or introduced manually, it was difficult to equalize their movement. Furthermore, the baits appeared to be stronger cues than the lights since the latter were exposed throughout the session, and trials were started with the introduction of the bait and were ended with its retraction.

At first, the observer was reluctant to use Method 2 because it was not known whether the squid could be attracted to the screen when presented by itself. To the surprise of the observer, the squid made clear approaches towards the positive screen presented with the light intensity the same as that of Pretraining 1. No approach was made towards the negative screen which was not lighted. This method was then applied for the rest of Pretraining 2 and

TABLE 2

Pretraining 1; Squid, *T. pacificus*, trained to feed at designated feeding area, (LS) left screen, (RS) right screen, (A) squid A, (B) squid B.

DAY	1		2		3		4	
Trial Number	LS	RS	LS	RS	LS	RS	LS	RS
1	A			A			B	
2				A				B
3	A			B	No		B	
4				B	response			B
5			B		at		B	
6	A			B	all			B
7	A			A			B	
8	B			B			B	
9	B		A				B	
10								B
11				A				
Total number of trial	10		11		11		10	
Attack level %								
Squid A	40		45		0		0	
Squid B	20		45		0		100	

$$\text{Attack level \%} = \frac{\text{Total response per squid}}{\text{Total number of trials}} \times 100$$

Note: Response means an attack on the bait presented at the feeding station.

for the succeeding simultaneous discrimination tests.

On training days, two and three, both squid easily discriminated between the positive and negative screens making perfect scores as shown in Table 3. Squid A with 12 attacks (60%) for day two performed better than squid B with 2 attacks (10%). The low level of attacks by squid B was not considered in the analysis of percentage of correct attacks. However, on day three, squid B recovered by attacking 70% of the time, all of which were correct. For day two, only the positive screen was presented (Figure 4c). Here the situation was simple, and as expected squid A made no mistake making clear approaches toward the positive screen. On day three, both screens (Figure 4d) were presented simultaneously and both squid made no mistake.

SDT using white lights with different intensities. Differences in intensity also serve as cues in stimulus discrimination in addition to wavelength difference. The next set of experiments was designed to determine the intensity level (expressed in terms of neutral density filters) at which squid stop differentiating. Figure 5 illustrates the combination of screens used.

Experiment SDT 1-1 (Figure 5a). This is an extension of Pretraining 2, Day 3 using the same pair of screens. The performance of each squid for two days is presented in Table 4. Again, the two squid made no mistake except for once by squid A on day two which is negligible.

Experiment SDT 1-2 (Figure 5b). Both screens were lighted with the light source of the negative screen masked by a 1.5 NDF. The light of the positive screen masked by O.5 NDF was the same as in the previous experiment. The results of the one day test are presented in Table 5. Squid B made a perfect score while squid A had 75% correct response which is still statistically significant.

In this experiment the intensity difference between the screens presented was about 26 times and here the squid made clear discrimination within a one day test. A typical approach

TABLE 3

Pretraining 2; test on the learning ability of the squid, *T. pacificus*; (LS) left screen, (RS) right screen.

DAY	2		3	
Trial Number	LS	RS	LS	RS
1	–	+	–	+
2	+	–	+B	–
3	+	–	+BA	–
4	–	+A	–	+AB
5	+	–	+B	–
6	–	+A	–	+AB
7	+A	–	+	–
8	+A	–	+	–
9	–	+A	–	+AB
10	+	–	+AB	–
11	–	+A		
12	–	+A		
13	+AB	–		
14	–	+B		
15	+A	–		
16	–	+		
17	–	+A		
18	+A	–		
19	–	+A		
20	+	–		
Total responses				
Squid A	5(+)	7(+)	2(+)	3(+)
Squid B	1(+)	1(+)	4(+)	3(+)
Total number of trials	20		10	
Attack level %				
Squid A	60		50	
Squid B	10		70	
Correct responses %				
Squid A	100		100	
Squid B	–		100	

$$\text{Correct response \%} = \frac{\text{Total response to positive screen}}{\text{Total response}} \times 100$$

Note: Day one (1) of training was devoted to the testing of Methods 1 and 2 (see results).

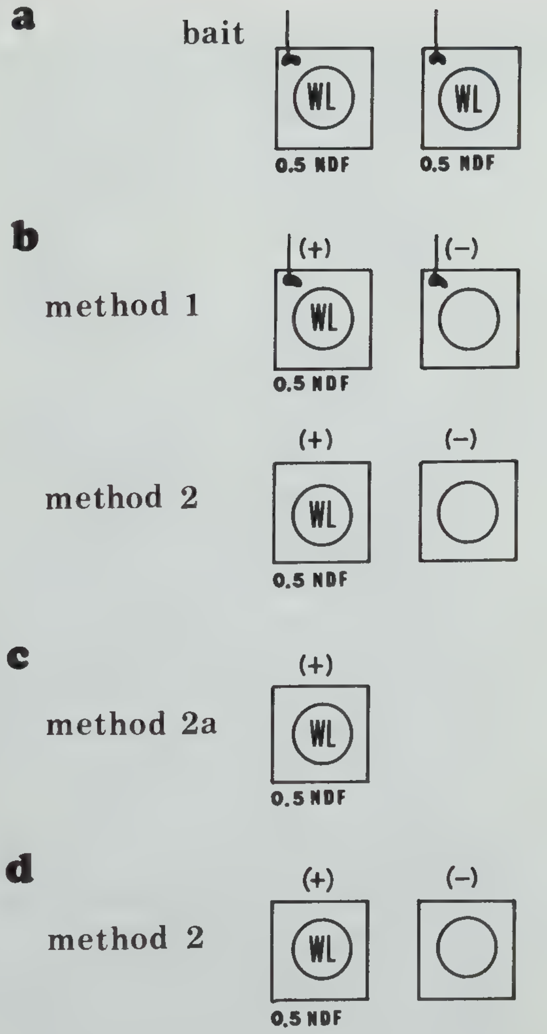

Figure 4. Screens presented for Pretraining Test; (WL) white light, (+) positive screen, (–) negative screen, (NDF) neutral density filter; (a) for Pretraining 1, day 1-4, (b) for Pretraining 2, day 1, (c) for Pretraining 2, day 2, and (d) for Pretraining 2, day 3.

where discrimination was clear is shown in Figure 7 (p. 222). In these cases, the squid made an almost straight approach towards the positive screen from the starting position. When the squid was about 10 to 20 cm away from the screen, it paused. At this position, the negative screen at the other side of the partition was no longer visible. Any reinforcement given at this position would be related only to the screen approached.

The pause in front of the screen allowed the observer to introduce the bait. It is interesting to note that later in the experiment, when the reward was delayed, the squid would continue moving toward the screen its arms open as if for

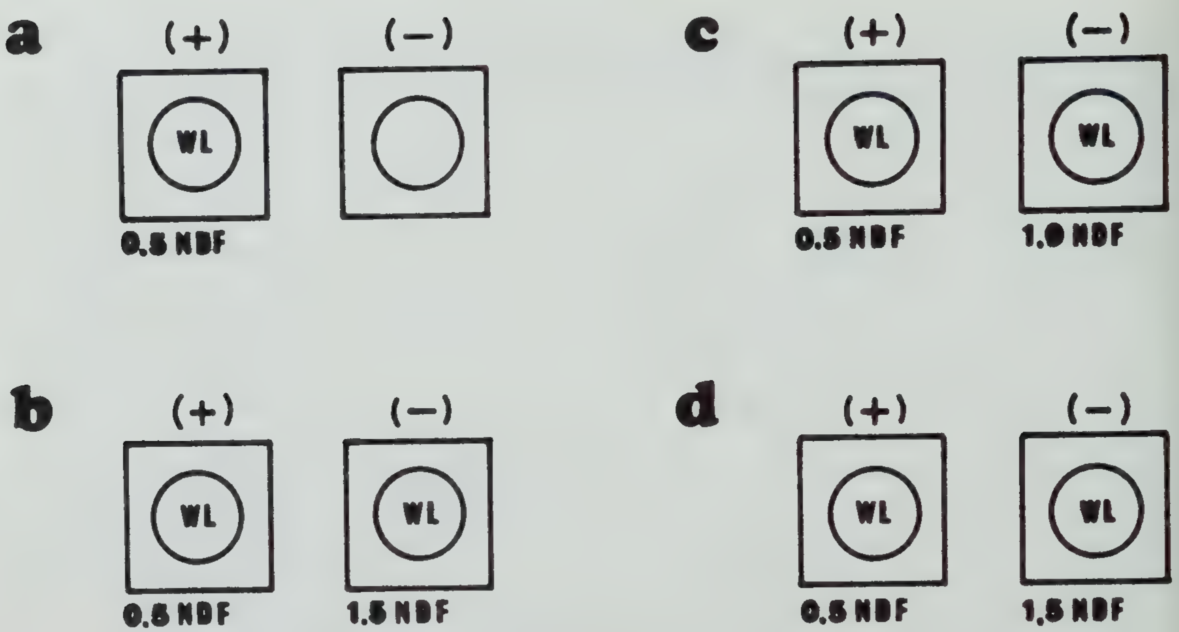

Figure 5. Screens presented for simultaneous discrimination test (SDT) using white light (WL) of different intensities; (+) positive screen, (−) negative screen, (NDF) neutral density filter; (a) SDT 1-1, (b) SDT 1-2, (c) SDT 1-3, and (d) SDT 1-4.

seizure. Messenger (1977a) in his study on the visual attack of the *Sepia* also observed that the animal paused after approaching a live bait (prawn). After about 10 seconds the cuttlefish seized the prawn by tentacle ejection. In *T. pacificus*, the pause though shorter was also followed by seizure but using its arms. When the bait sunk near the side of the screen, the squid would yaw head first towards the bait and seized it.

Experiment SDT 1-3 (Figure 5c). In this test, the light intensity difference was reduced with the light source of the negative screen masked by a 1.0 NDF. The positive screen was four times brighter than the negative screen. The results of this two-day experiment, tabulated in Table 6, indicated that the two squid were not able to discriminate. During day one of experimentation, squid A performed at chance level of 55% correct responses while squid B performed at 72% which is above chance level. On day two, squid B now performed at chance level of 40% while squid A had 10% correct responses.

TABLE 4

Simultaneous discrimination test (SDT) 1-1; discrimination between a lighted screen (+) and an unlighted screen (−); (LS) left screen, (RS) right screen.

DAY	1		2	
Trial Number	LS	RS	LS	RS
1	+	−	+A	−
2	+	−	−	+A
3	−	+A	+	−A
4	+AB	−	−	+BA
5	−	+	−	+BA
6	−	+A	+B	−
7	+B	−	−	+AB
8	−	+B	+B	−
9	+	−	−	+BA
10	−	+B	+B	−
11	−	+B		
12	+B	−		
13	−	+B		
14	+	−		
15	−	+		
16	−	+		
17	+	−		
18	+	−		
19	+	−		
20	−	+		

TABLE 4 continued

Total responses				
Squid A	1(+)	2(+)	1(+)	5(+), 1(−)
Squid B	3(+)	4(+)	3(+)	4(+)
Total number of trials	13		10	
Attack level %				
Squid A	23		70	
Squid B	50		70	
Correct responses %				
Squid A	100		85	
Squid B	100		100	

In this experiment, the nature of approaches were different from approaches where discrimination was possible. Figure 7 also shows examples of two approaches in which the squid was not able to discriminate. In one case (-o-), the squid went from the starting position straight towards the partition. During this type of approach, both screens are probably visible to the squid, producing equal stimulation. When about 30 cm away from the partition, the squid made a turn to either screen. In a few instances the squid continued swimming straight forward and bumped into the edge of the partition. In the other case (-x-), the squid initially advanced toward one screen and then turned toward the other screen only to turn back the former screen.

Experiment SDT 1-4 (Figure 5d). To test whether *T. pacificus* could be retrained to discriminate white light of different intensity, the conditions in Experiment SDT 1-2 were repeated. The tests were conducted over 4 days with results shown in Table 7. Squid B was able to discriminate at 90% correct responses by day four.

SDT using green and blue lights.
Results from the series of experiments using white lights of different intensities show that the squid could not differentiate between a white light with 0.5 NDF and another white light with 1.0 NDF. With the above information, it was then safe to present colored lights even though they produced slight differences in intensity.

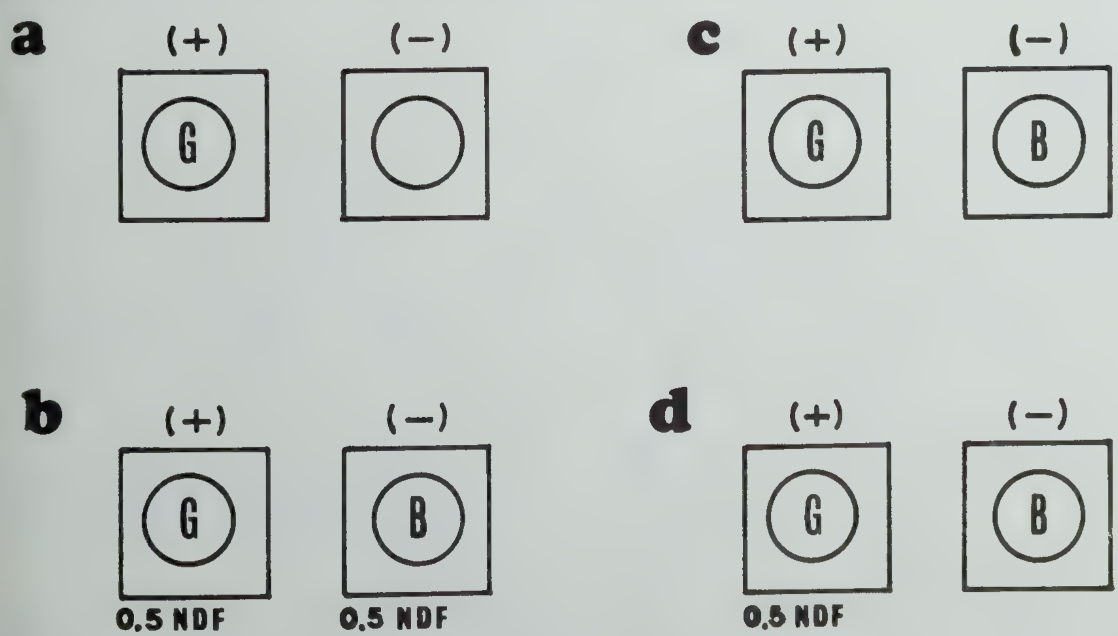

Figure 6. Screens presented for simultaneous discrimination test (SDT) using green and blue lights; (+) positive screen, (−) negative screen, (NDF) neutral density filter; (a) SDT 2-1, (b) SDT 2-2, (c) SDT 2-3, and (d) SDT 2-4.

Table 5

Simultaneous discrimination test (SDT) 1-2; discrimination between a white light with a 0.5 neutral density filter (+) and a white light with a 1.5 neutral density filter (−); (LS) left screen; (RS) right screen.

DAY	1	
Trial Number	LS	RS
1	−	+AB
2	+	−A
3	−	+BA
4	−	+B
5	+	−
6	+	−
7	+B	−
8	−	+A
9	−	+AB
10	+	−A
11	+AB	−
12	−	+AB
Total responses		
Squid A	1(+)	5(+), 2(−)
Squid B	2(+)	5(+)
Total No. of trials	12	
Attack level %		
Squid A	66	
Squid B	58	
Correct responses %		
Squid A	75	
Squid B	100	

Table 6

Simultaneous discrimination test (SDT) 1-3; discrimination between a white light with a 0.5 neutral density filter (+) and a white light with a 1.0 neutral density filter (−); (LS) left screen, (RS) right screen.

DAY	1		2	
Trial Number	LS	RS	LS	RS
1	+A	−	−AB	+
2	−B	+A	−	+B
3	−	+BA	−	−BA
4	+B	−A	+	−BA
5	+B	−	−	+B
6	−A	+B	+B	−A
7	−	+B	−B	+A
8	−	+BA	+	−AB
9	+A	−B	+	−AB
10	+	−BA	−	+B
11	−A	+B		
12	+B	−		

Table 6 continued

Total responses				
Squid A	2(+) 2(−)	3(+) 2(−)	1(−)	1(+) 5(−)
Squid B	3(+) 1(−)	5(+) 2(−)	1(+) 2(−)	3(+) 4(−)
Total number of trials	12		10	
Attack level %				
Squid A	75		70	
Squid B	91		100	
Correct responses %				
Squid A	55		10	
Squid B	72		40	

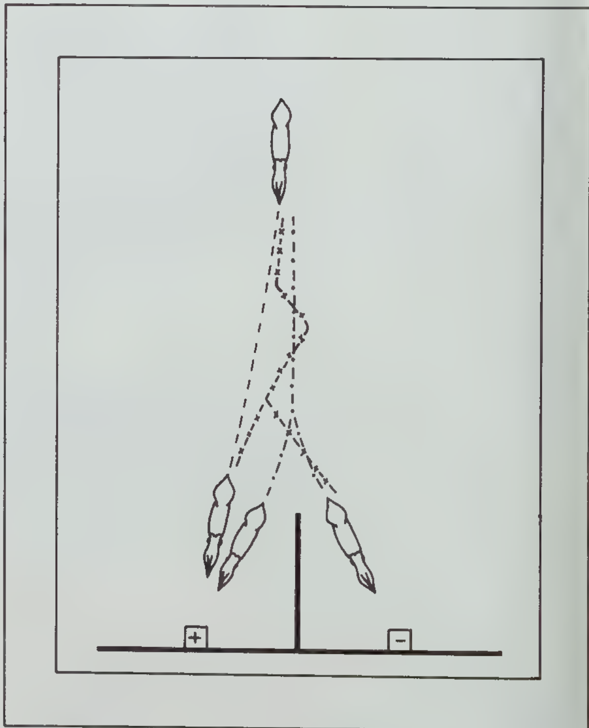

Figure 7. Examples of typical squid approaches to positive (+) or negative (−) screen; (---) a clear approach to positive screen, (-··-) and (-x-) approaches which could be directed to either screen.

The green light, with higher transmissivity maximum (45%), appeared brighter than the blue light (41.3%).

Experiment SDT 2-1 (Figure 6a). In order to establish a positive image the green light was presented together with an unlighted screen.

TABLE 7

Simultaneous discrimination test (SDT) 1-4; rediscrimination between a white light with a 0.5 neutral density filter (+) and white light with a 1.5 neutral density filter (−); (LS) left screen, (RS) right screen.

DAY	1		2		3		4	
Trial Number	LS	RS	LS	RS	LS	RS	LS	RS
1	−A	+B	+	−A	−	+A	+AB	−
2	−	+A	−	+A	+	−A	+B	−
3	−	+A	−B	+A	+B	−A	−	+B
4	+B	−	−	+AB	−	+AB	−	+B
5	+BA	−	+B	−	−	+A	−	+B
6	−	+A	+	−B	−B	+A	+B	−
7	+	−B	−	+A	+AB	−	+B	−
8	−A	+B	+	−A	+B	−	−B	+
9	+	−AB	−	+A	−B	+A	+B	−
10	+	−A	+A	−	+B	−A	+B	−
11	+	−A			+B	−A		
12	−	+AB			−B	+A		
13	−	+AB			+A	−B		
14	−	+B			+B	−A		
15	+B	−						
16	+A	−						
Total responses								
Squid A	2(+) 2(−)	5(+) 3(−)	1(+)	5(+) 2(−)	2(+)	6(+) 5(−)	1(+)	0 0
Squid B	3(+)	5(+) 2(−)	1(+) 1(−)	1(+) 1(−)	6(+) 3(−)	1(+) 1(−)	6(+) 1(−)	3(+)
Total number of trial	16		10		14		10	
Attack level %								
Squid A	75		80		93		10	
Squid B	62		40		78		100	
Correct responses %								
Squid A	58		75		62		LOW	
Squid B	80		50		63		90	

TABLE 8

Simultaneous discrimination test (SDT) 2-1; discrimination between a lighted screen (+) using green light (523.5 nm) and an unlighted screen (−); (LS) left screen, (RS) right screen.

DAY	1		2	
Trial Number	LS	RS	LS	RS
1	+AB	−	−	+AB
2	−	+AB	+AB	−
3	+B	−A	−	+BA
4	−	+AB	−	+AB
5	−	+AB	−	+AB
6	−B	+A	+AB	−
7	+AB	−	+AB	−
8	+AB	−	+AB	−
9	+AB	−	−	+AB
10	−	+AB	+AB	−
Total responses				
Squid A	4(+) 0	5(+) 1(−)	5(+) 0	5(+) 0
Squid B	5(+) 1(−)	4(+) 0	5(+) 0	5(+) 0
Attack level %				
Squid A	100		100	
Squid B	100		100	
Correct responses %				
Squid A	90		100	
Squid B	90		100	

Both squid responded to all trials presented during the two-day test as tabulated in Table 8. The performance of both squid were the same making 90% correct responses on day one 100% on day two.

TABLE 9

Simultaneous discrimination test (SDT) 2-2; discrimination between positive screen (+) with green light (523.5 nm) and negative screen (−) with blue light (450 nm) both masked with 0.5 neutral density filters; (LS) left screen, (RS) right screen.

DAY	1	
Trial Number	LS	RS
1	−B	+A
2	+B	−A
3	−B	+A
4	+B	−A
5	−B	+A
6	−B	+A
7	−B	+A
8	+B	−A
9	+B	−A
10	+AB	−
Total responses		
Squid A	1(+)	5(+)
	0	4(−)
Squid B	5(+)	0
	5(−)	0
Attack level %		
Squid A	100	
Squid B	100	
Correct responses %		
Squid A	60	
Squid B	50	

TABLE 10

Simultaneous discrimination test (SDT) 2-3; discrimination between positive screen (+) with green light (523.5 nm) and negative screen (−) with blue light (450 nm); (LS) left screen, (RS) right screen.

DAY	1		2	
Trial Number	LS	RS	LS	RS
1	+B	−A	−B	+A
2	−AB	+	−A	+B
3	−	+AB	−	+AB
4	−A	+B	+B	−
5	+A	−B	+A	−B
6	+B	−A	+	−AB
7	+	−A	−A	+B
8	−	+AB	+	−AB
9	+	−AB	−A	+B
10	−AB	+	+A	−B

TABLE 10 continued

Total responses				
Squid A	1(+)	2(+)	2(+)	2(+)
	3(−)	4(−)	3(−)	2(−)
Squid B	2(+)	3(+)	1(+)	4(+)
	2(−)	2(−)	1(−)	4(−)
Attack level %				
Squid A	100		90	
Squid B	90		100	
Correct responses %				
Squid A	30		44	
Squid B	55		50	

Experiment SDT 2-2 (Figure 6b). To test color discrimination a green positive screen was matched against a blue negative screen with both light sources masked by 0.5 NDF. One day test showed both squid performing at chance level for this situation as tabulated in Table 9.

Experiment SDT 2-3 (Figure 6c). To produce a brighter screen for this experiment, the 0.5 NDF were removed for both screens. The two day tests demonstrated that again, the two squid performed at chance level as tabulated in Table 10.

Experiment SDT 2-4 (Figure 6d). In this experiment, the light source of the green screen was masked with a 0.5 NDF, while the blue shape had none. This final series of test was conducted over four days, and the results tabulated in Table 11 clearly indicated that the squid were not able to discriminate between the two colors.

Discussion

Studies on discrimination learning in octopus are always done with the test animal in isolation. This was not followed since the squid, *T. pacificus*, in isolation as observed in holding tanks were not feeding well and were seen repeatedly hitting the walls with their fins. In the experiments, the response of one squid to screens presented did not affect the response of the other. As early as day 2 and 3 in Pretraining 2, it could be seen that an approach of one squid on a screen was not always followed by the other. There were individual approaches as well as approaches in pair. Two baits were always made ready before each trial so that each squid can be given its share when both

TABLE 11

Simultaneous discrimination test (SDT) 2-4; discrimination between positive screen (+) with green light (523.5 nm) masked with a 0.5 neutral density filter, and negative screen (−) with blue light (450 nm); (LS) left screen, (RS) right screen.

DAY	1		2		3		4	
Trial Number	LS	RS	LS	RS	LS	RS	LS	RS
1	−B	+A	−A	+B	+	−A	+A	−
2	−A	+B	+B	−A	+	−	+	−AB
3	+	−AB	+	−AB	+A	−	−B	+A
4	+A	−B	+	−A	−	+A	+B	−A
5	+A	−B	−A	+B	+A	−	−	+B
6	−AB	+	+A	−B	−A	+	+B	−
7	+AB	−	−A	+B	+	−	−B	+
8	−A	+	+A	−	−	+A	−B	+
9	+AB	−	−AB	+	−A	+	−B	+
10	−	+AB	−A	+	−	+A	+B	−
Total responses								
Squid A	4(+)	2(+)	2(+)	3(−)	3(+)	3(+)	1(+)	1(+)
	3(−)	1(−)	5(−)	0	2(−)	1(−)	0	2(+)
Squid B	2(+)	2(+)	1(+)	3(+)	0	0	3(+)	1(+)
	2(−)	3(−)	1(−)	2(−)	0	0	4(−)	1(−)
Attack level %								
Squid A	100		100		90		40	
Squid B	90		70		0		90	
Correct responses %								
Squid A	60		20		66		50	
Squid B	44		57		0		44	

squid made a correct approach to a positive screen.

The learning ability of the squid was established when it made discriminations between screens presented with different intensities (SDT 1-1 and 1-2). The same rapid learning ability is also displayed by the octopus (Messenger & Sanders, 1972) where after only four sessions, all octopuses in the one-cue experiment made brightness discriminations at a level significantly above chance. This learning ability of the squid was further demonstrated when it discriminated screens previously presented (SDT 1-4) after going through a two-day test (SDT 1-3) where it was not to discriminate. Similar behavior was also observed for octopus where after a non-discrimination stage using violet/grey vertical rectangles, the animal was able to discriminate reintroduced black/white vertical rectangles (Messenger, 1977b).

In Experiment SDT 2-1 where an unlighted screen was presented together with a screen with green light projected, there were two contrasting cues, one was the big difference in intensity and the other was color. Using the two cues, even an animal without color vision can still distinguish one screen from the other using the intensity difference as the cue which is similar to the situation in Experiment SDT 1-1. The high percentage of correct attacks even for the first session suggest that the squid was using intensity difference and not color as the primary cue.

Assuming that the squid was using color as the cue, it would be difficult to attain a high percentage of attacks at the very start of experimentation since the squid would be viewing the colored screen as a new image. In the pretraining sessions, it took four days before a squid was able to attain a 100% attack level. During this period, the squid was getting itself accustomed to the white light projected on the screen and associating it with the bait presented simultaneously. Therefore, it appears that a new screen, presented without the presence of bait, requires a period for learning the conse-

quences of an approach to this screen. But, without color vision, this colored screen would only appear as a lighted screen, brighter than the unlighted screen which would be a condition similar to Experiment SDT 1-1. Thus the 100% attack level and 90% correct responses were attained by the squid at the first session and then perfected in the session that followed. The nature of approaches here was the same with those of SDT 1-1 and other experiments where discrimination was possible.

For color discrimination test using blue and green lights projected on screens, at first both colored lights were masked by 0.5 NDF with the intention of presenting them at low intensity. The results were not significant with both squid making aproaches to either screen in all trials. To increase the light intensity, the neutral density filters were removed. Again, the squid responding to almost all trials showed familiarity to both screens presented. Even at higher intensities, the performances were not significant. Recall that at these conditions, the green screen appeared slightly brighter than the blue screen. But this difference in intensity was not enough for the squid to discriminate between the screens presented. In the final experiment (SDT 2-4) with the green screen masked by 0.5 NDF to lessen the intensity difference, the results for four sessions were the same as those of the previous experiments.

Fehring (1972) in hue discrimination experiments used a similar technique on loggerhead turtles which were suspected to have color vision. He reported fast discrimination with most specimens making perfect scores after only two days. Since *T. pacificus* rapidly learned to discriminate in intensity discrimination tests (SDT 1-1 and 1-2), then if the squid possessed color vision, they should have learned at about the same rate during the color discrimination tests (SDT 2-2, 2-3, and 2-4).

The findings in the present study agree with the work of Orlov and Byzov (1962). With regard to color vision, *T. pacificus* and *O. vulgaris*, studied by Messenger *et al.* (1973) and Messenger (1977b, 1979), are the same. With regard to squid fishing, the use of colored underwater lights does not seem practical in view of the findings in this study. Since both colored and white lights are treated similarly by the squid, it is not necessary to expend the extra energy to produce colored lights.

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A REVIEW OF CEPHALOPOD FISHERIES BIOLOGY

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Abstract

The status of knowledge of the biology of cephalopods applicable to fisheries management is reviewed, especialy relating to life span, age at maturity, fecundity, spawning, recruitment, migration, populations and prey/predator relationships. Data are summarized and major areas of lack of information are indicated. It is concluded that probably no species of squid or octopus has been sufficiently studied to afford proper data for management. Of approximately 650 species of cephalopods some data are available for only 23 species or about four per cent, some of which have no commercial value. The need for support of biological studies relating to the fisheries is stressed.

Introduction

A basic tenet of fisheries science is that stocks cannot be meaningfully managed without a solid basis of biological information on such factors as (1) life span, (2) age at maturity, (3) fecundity, (4) spawning, (5) recruitment, (6) migrations, (7) populations, and (8) prey/predator relationships.

If information on all or most of these subjects is necessary, then very few of the actual or potential commercial species of cephalopods have been sufficiently studied, as such data are unavailable. Fisheries officers may well question why data necessary for stock management are not available but the answer is simple; most cephalopod fisheries are relatively new and governments have allocated few funds for studies of a fishery that, except in one or two countries, is still not considered to be of major economic value. This view is now changing because of the increasing value of the fisheries. The following account is an attempt to review briefly the present status of the fisheries biology of cephalopods so that we may identify the gaps in our knowledge and make plans for future research.

Fisheries Biology

Japan, almost alone of the fisheries nations, has conducted biological studies of commercial species of cephalopods. This is understandable when one considers that for years Japan has been the major world consumer of both squid and octopus. Indeed, the world squid fisheries are primarily dependant upon the Japanese market and only secondarily upon the demands of Spain, Portugal, Italy, Greece, and recently the Soviet Union. Only in the last ten to fifteen years have other western nations, France, England, Germany, Poland, certain South American nations, Mexico, and the United States begun to realize the importance of cephalopods, either for their own consumption or because of interest in the Japanese market. But all of these nations are consumers and have little regard for management or resource conservation. This attitude is a result of several widely held premises among which the most common are beliefs that cephalopods represent a one year crop which will be wasted if it is not harvested, and that the supply is nearly inexhaustible. Thus there has been little incentive for the kinds of fisheries studies long undertaken on fin fish. Only when wide fluctuations in stocks appeared and fishing vessels were forced to go further and further afield did even the Japanese begin to undertake squid studies.

In the United States and Canada squid have been harvested for many years either for bait or for fish meal. As a result the price to the fisherman was low and agencies were uninterested in supporting fisheries investigations. In the last five years or so the picture has changed and much interest is being shown in the squid fisheries. Squid biology related to the fisheries, however, is still fragmentary and in its infancy.

On the other hand, scientists in France, England and the United States have long been interested in cephalopods for different reasons. Their interests have been based upon elucidating basic biological information: physiology, biochemistry, neuro-physiology,

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behaviour, genetics, phylogeny, systematics, zoogeography and others. This interest has been generated by medical importance, the search for basic scientific knowledge, and heuristic approaches. The great advances in the last decade in rearing and maintaining squid and octopus have not been primarily from attempts to aid mariculture but to provide animals for research.

Thus we see that there has been a polarization of research efforts, one based upon applied fisheries needs and the other on basic research and medical requirements. It is time that these two reservoirs of biological data are brought together and integrated for the mutual benefit of both interests.

This review draws heavily upon information from studies conducted at three widely separate areas: Newfoundland on *Illex illecebrosus*, California on *Loligo opalescens*, and Japan on *Todarodes pacificus*. The California study was the only planned, broad, biological program done purely for fisheries management in the United States. From lack of funds it was terminated after three years just as the program was beginning to yield useful results (Recksiek & Frey, 1978). The Japanese have led the field in squid studies and numerous papers have appeared in Japanese journals on practically all phases of squid biology related to the fisheries. Many of these are mentioned in FAO Fisheries Technical Paper 173 (Okutani, 1977). Most, however, are in Japanese with only brief English abstracts and are of limited value for western workers.

An indication of the growing interest in the cephalopod fisheries is the appearance in the last ten years of four major reviews of the fisheries on a world wide basis (Arnold, 1979; Okutani, 1980; Voss, 1973, and Zuev & Nesis, 1971). Another valuable aid for fisheries biologists has been the publication of the FAO Identification Sheets for the various fishing fishing areas of the world (Roper, 1977; Roper & Sweeney, 1982).

The following pages review the problem areas in our knowledge as given in the Introduction.

Life Span. There is little solid information on the age and life span of cephalopods. No reliable method has so far been developed for aging either squid or octopus. Most data on age have been derived either from rearing studies or from length/weight frequencies and size at maturity. Aquarium studies, until recently, have been conducted mainly on octopods. *Octopus vulgaris*, as well as other species, can be easily maintained and will spawn and brood their eggs in aquaria. Usually the female dies after her eggs have hatched. Because the females attain sexual maturity in one year or less, mate, brood their eggs, and die, it has been assumed that the females live for only one year. It has been axiomatic that female octopus do not feed during egg brooding, waste away and die, despite occasions on which the females fed and continued to live. So general has the belief become that some females die after their brooding in aquaria is finished because they have been starved to death.

Probably in nature some octopus live to brood several times and to attain a much larger than average size. Operations on the optic gland (Wodinsky, 1977 and pers. comm.) may prevent sexual maturity and the animals may live to considerable age and attain great size. Possibly the very large animals occasionally reported may represent those in which sexual maturity has been repressed. It may also be that they are animals that have survived several spawnings. Small octopus such as *O. hummelincki*, a tropical western Atlantic species, frequently live after brooding (Reisinger, unpubl. data).

The other method of aging is by sampling populations to obtain either length frequencies or weights or both over considerable time periods, mostly from the commercial fisheries. It is thus possible to follow the young squid through the year, assess their monthly growth and determine when they have reached maturity. This method is standard practice in squid studies but also has its drawbacks. Size at maturity is not necessarily representative of life span unless one assumes that squid die after mating and spawning and that they spawn only once. This assumption is based primarily upon the many records of mating/spawning frenzies in *Loligo opalescens* in California as reported by Fields (1950), McGowan (1954) and others.

This kind of aggregation and frenzy has not been reported for other species and may be atypical. Length and weight frequencies may also become less reliable and fail completely as far as age is concerned as immature animals enter the mature population and size groups are lost in the adult weight and length ranges.

The importance of an accurate aging method has long been recognized and attempts have been made to use the few hard structures of teuthoids, their beaks, gladius, sucker rings, and statoliths, by searching for growth rings comparable to those found on fish scales and otoliths. Statoliths are the only structures so far that have shown possibilities but considerable difficulties are encountered in interpretation of rings in certain areas of the statoliths (Spratt, 1978; Kristensen, 1980). Nonetheless, this structure is promising and may soon prove useful.

The cuttlebone of *Sepia* was first shown to be of value in aging by Choe (1963) who found that in aquaria and large cisterns a chamber or striation was laid down every one to three days and could thus yield a fairly reliable age determination. Boletzky (pers. comm.) is now working on this and the effects of various factors on the deposition of chambers using European cuttlefish.

Realizing that no definitive method has been developed, Table 1 has been derived from references in the literature. Examination of these data shows that cephalopods in general appear to have an average life span of one to two years but that, depending upon the species, it may range from about four months or less to five years or longer. Small species such as *Octopus joubini*, and probably the pygmy cuttlefish *Idiosepius*, and other small forms are very short lived and may produce one to two or even three generations a year. The estimated ages of *Octopus vulgaris* based on size may be due to abundant food and fast growth as appears to be the case with the giant *Octopus dofleini* of the North Pacific.

Even though *Loligo opalescens* dies shortly after mating and spawning, age estimates both by length frequencies and statolith examination indicate that they live for one to about three years. Studies on *Loligo pealei* and *Illex illecebrosus* also indicate this age range. This has been explained by Summers (1971) and Mesnil (1977) as a result of winter/spring or summer/fall spawning. In the first case the females would spawn at one year of age or thereabouts while in the second case conditions would delay or inhibit growth in the late hatchlings so that they would not mature until the following summer and would spawn at an age of one and half to two years of age or even later.

The age of oceanic squid has not been determined using statoliths and has depended upon estimates resulting from frequency curves. No one has attempted to estimate the ages of the giant squid *Moroteuthis* or *Architeuthis*. Although nothing is known of age at spawning, females of midwater squid such as *Chaunoteuthis* and some of the cranchiids show strong mantle deterioration; the wall becomes soft and flabby, and it appears that these females do not recover and also die shortly after spawning.

The ages of deep-sea squid and octopods are unknown. Possibly reduced metabolism in cold waters and low food availability may contribute to longer life spans. The question cannot be resolved at this stage of our knowledge.

It is obvious that special effort is required to attempt to resolve the age question before satisfactory fisheries models can be constructed.

Age at Maturity. This has two built-in difficulties: determining age as discussed above, and recognizing sexual maturity or stages thereof.

Sexual maturity in males is usually considered to occur when spermatophores are found in Needham's sac. Studies now being conducted at Miami by Hess indicate that the first spermatophores manufactured may be incomplete and that the male makes spermatophores over a considerable period of time (Hess, pers. comm.). It is obvious that the sperm in the earliest spermatophores must either have an inhibitor or a long viability in order for them to remain active until spermatophore manufacture is completed and the male is functionally "mature". Body growth continues throughout the time of spermatophore construction so that from initiation

TABLE 1

Estimated life span of selected species of cephalopods based upon various methods of analysis found in the literature.

Species	Estimated span	Method	Authority
SEPIOIDEA			
Sepia officinalis	2-3 years	?	Mangold, 1963
S. orbignyana	1-1½ years	length frequencies	Mangold, 1963
S. elegans	1 year	length frequencies	Mangold, 1963
Rossia macrosoma	1 year plus	length frequencies	Mangold, 1963
Sepiola rondeleti	1 year ?	?	Mangold, 1963
Sepietta oweniana	less than 1 year ?	length frequency	Mangold, 1963
TEUTHOIDEA			
Loliginidae			
Loligo vulgaris	males 3-4 yrs., females 2-3 years	?	Mangold, 1963
L. forbesi	1 year	length frequency	Holme, 1974
L. pealei	1-1½ years	length frequency	Hixon, 1980
	14-24 months, Max. 36	length frequency	Summers, 1971
L. opalescens	1-1½-3 years	length frequency	Authors
	1-1½-3 years	statoliths	Spratt, 1978
Doryteuthis plei	1-1½ years	length frequency	Hixon, 1980
Sepioteuthis sepioidea	less than 1 year	rearing	LaRoe, 1971
Lolliguncula brevis	1-1½ years	length frequency	Hixon, 1980
Alloteuthis media	M, 1 year, F, 1-1½ years	?	Mangold, 1963
Ommastrephidae			
Illex illecebrosus coindeti	M, 12-20 months, F, 24 months	?	Mangold, 1963
Illex i. illecebrosus	1-2½ years	length frequency	Mesnil, 1977
Todaropsis eblanae	M, 24 months; F, 2-3 years	?	Mangold, 1963
Todarodes pacificus	1 year	length frequency	Hamabe & Shimizu, 1966
Ommastrephes bartrami	1 year	length frequency	Araya, this volume
O. pteropus	1 year	length frequency	Hixon *et al.*, 1981
Dosidicus gigas	16-20 months	length frequency	Ehrhardt *et al.*, this volume
OCTOPODA			
Octopus vulgaris	1-5 years, av. 2 years	length frequency	Mangold, 1963
O. salutii	2 years to maturity	length frequency	Mangold, 1963
O. briareus	12-15 months	rearing	Wolterding, 1971
O. joubini	4-12 months plus	rearing	Thomas & Opresko, 1973
Eledone cirrhosa	M, 14-15 months, F, 16-18 months	length frequency	Mangold, 1963
Bathypolypus sponsalis	2 years	length frequency	Mangold, 1963

of spermatophore production to completion, size increases steadily.

Whether, for fisheries purposes, maturity should be considered to be whenever one or any spermatophores are present or only when the sac is full is open to discussion. The average number of spermatophores in adult males ready to mate has been determined for very few species of squid. Also the number varies greatly from group to group. In octopods the number of spermatophores may be very high in some species (more than 100) while in others only one or two may be produced. The process of spermatogenesis in *Loligo opalescens* has been described by Grieb and Beeman (1978).

Maturity in females is also difficult to determine. Females of some species produce thousands of eggs while others may produce only a dozen or so. The degree of maturity is difficult to determine and each species requires careful study. Size of the eggs, size of the ovary, size and condition of the nidamental glands and accompanying colour changes are all possible indicators.

In view of the difficulties described above as to when males and females are actually sexually

mature, the assessment of age at this stage is more difficult. In examining Table 1, it can be seen that in general males may have a shorter estimated life span than females. This is based on the postulation that males die shortly after mating, which happens in *Loligo opalescens* (McGowan, 1954), but not necessarily so in others, and that the females have a delay between mating and spawning and may spawn over a number of days or weeks. In octopods the life span may be longer because the females brood their eggs for up to two months or more after spawning and may live for weeks to months thereafter. Thus for the females, age at sexual maturity may be considered about equal to the age of males at death in those species in which the males die after mating.

Correlation of sexual maturity with mantle length may afford a means of aging species when aquarium rearing studies have provided growth data, although all aquaria studies must be viewed with caution.

Fecundity. Fecundity is usually determined by counting the number of eggs contained in the ovary of mature females. If the species is one that spawns completely in either one spawning or in several spawnings over a short period, this method of establishing fecundity may be reliable. This condition may possibly be determined if all of the eggs in the ovary are at the same or nearly the same stage of development. The presence of eggs of various sizes and stages usually indicates a prolonged spawning period during which new eggs may be produced and others have the time to develop. In this latter case egg counts at any one time may be very misleading.

Hixon (1980) reported that *Lolliguncula brevis*, a one time spawner, laid 2 024 eggs in the laboratory (previous estimates 1 400-6 350). Three female *Loligo pealei*, also in the laboratory, laid 21 315-53 072 and 55 308 eggs respectively over periods of from 5 days to one month. Previous estimates of from 980-15 000 were made from egg counts (Haefner, 1959; Summers, 1971) or by gravimetric extrapolation (Vovk, 1972). Another loliginid, *Doryteuthis plei*, was determined to spawn 14 310 eggs by spawned egg count (Roper, 1965) and 218-2 500 by ripe egg count (LaRoe, 1967). It can be seen from these figures that fecundity based upon egg count can be off by several orders of magnitude unless it is known whether it is a one time (several days) spawner or whether it spawns over one or more months.

Examination of Table 2 shows that cephalopods may spawn as few as 25 eggs or as many as 6 000 000 eggs. These numbers depend primarily upon either the absolute size of the eggs as in *Octopus maya* which is a large octopus that produces large eggs (17 mm long), or the relative size as in *Idiosepius pygmaeus* that is the smallest cephalopod known (mantle length 8 mm) and produces eggs less than 1 mm long. All of the species producing large numbers of eggs (greater than 5 000) have small eggs (less than 3 mm), but within this group the size of the eggs may vary. As a general rule, the greater the number of eggs, the smaller they are. Unfortunately, as can be seen from the table, little information is available on fecundity and much that is given here is subject to reservation.

Spawning. Spawning time, place, and mature eggs are known for very few species of squid. Information in nearly all species is fragmentary and much of the available information is derived from catch statistics from which deductions have been made.

The spawning of cuttlefish has been recorded from classical times. *Sepia officinalis* spawns nearly or entirely around the year, coming into shallow water and attaching the eggs one at a time to hard objects on the bottom. Many other cuttlefish follow the same pattern. Grimpe (1928) wrote that *Rossia macrosoma* spawned around the year on the northern European coast and the North Sea, fixing its eggs to hard objects on the bottom. *Idiosepius*, according to Natsukari (1970) is a summer spawner but it is possible that it has several generations a year.

Despite the long interest in *Loligo*, its biology has been little studied. According to Tinbergen and Verwey (1945) *Loligo vulgaris* spawns in the summer in Dutch waters but Holme (1974) could not verify that it spawned in the English Channel. *Loligo forbesi* has its major spawning in Great Britain in December and January (Holme, 1974), coming into shallow water and attaching the eggs to objects that keep them off

TABLE 2

Fecundity of various species of cephalopods, derived from the literature.

Species	Number of Eggs	How Determined	Source
SEPIOIDEA			
Sepia officinalis	about 1000	egg count	Mangold, 1963
Rossia macrosoma	about 40	egg count	Mangold, 1963
Idiosepius pygmaeus	25-64	eggs spawned	Natsukari, 1970
TEUTHOIDEA			
Loliginidae			
Loligo vulgaris	about 6000	egg mops	Mangold, 1963
L. pealei	21 315-55 308	egg mops	Hixon, 1980
L. Opalescens	14 000	egg mops	Fields, 1965
Doryteuthis plei	14 310	egg mops	Roper, 1965
Lolliguncula brevis	1400-6360	egg count	Hixon, 1980
Sepioteuthis sepioidea	260	egg count	Voss, unpubl.
Alloteuthis media	1000-1400	egg count	Mangold, 1963
Ommastrephidea			
Illex illecebrosus coindeti	5000-12 000	egg count	Mangold, 1963
	50 000-100 000	egg count	Boletzky *et al.*, 1973
Illex i. illecebrosus	440 000 plus	?	Durward *et al.*, 1979
Todaropsis eblanae	5000-10 000	egg count	Mangold, 1963
Todarodes sagittatus	12 000-15 000	egg count	Mangold, 1963
T. pacificus	70 000 mature eggs	egg count	Joo Youl Lim, 1967
T. filippovae	about 500 000	estimated	Dunning, 1981
Ommastrephes pteropus	52 618-186 461	egg count	Hixon *et al.*, 1980
O. caroli	360 000	?	Clarke, 1966
Dosidicus gigas	1-6 million	?	Ehrhardt *et al.*, this volume
OCTOPODA			
Octopus vulgaris	127 000-402 000	egg strings	Mangold, 1963
O. briareus	100-500	egg strings	Wolterding, 1971
O. joubini	40-95	egg strings	Thomas & Opresko, 1973
O. maya	1500-2000	egg strings	Solís, 1967
Eledone cirrhosa	1010-3800	egg count	Mangold, 1963
E. moschata	280-370	egg count	Mangold, 1963
Bathypolypus sponsalis	70-120	egg count	Mangold, 1963

the bottom. Aggregations have not been seen. *Loligo pealei* spawns in New England waters around May (Summers, 1971) but it may spawn later further south. In Texas it spawns in summer and fall (Hixon, 1980). Spawning is usually communal but not in major aggregations. The eggs are attached to the bottom in mops in shallow water. *Loligo opalescens* spawns in the winter in southern California but progressively later in the northern regions. It forms large spawning aggregations in shallow water and attaches its mops to hard objects on the bottom (Fields, 1965). *Loligo edulis budo* in Japan spawns late fall apparently offshore (Ikehara *et al.*, 1977). The tropical *Doryteuthis plei* spawns year round in Texas according to Hixon (1980). The Japanese *Doryteuthis kensaki* spawns in August attaching its egg mops to sandy bottom (Natsukari, 1976). *Doryteuthis bleekeri* (Matsui, 1974) spawns in inshore Japanese waters in December through May.

The east American *Lolliguncula brevis* spawns all year, attaching its eggs in mops in shallow estuarine areas (Hixon, 1980). The Caribbean Reef Squid, *Sepioteuthis sepioidea*, spawns all year round throughout its range (LaRoe, 1967), while the Australian calamary, *S. australis*, spawns from July through November (Potter, Winstanley & Caton, this volume); both attach their eggs to algae and rocks.

The time and place of spawning of the ommastrephids are practically unknown for any species. Almost all published information on spawning time is based upon capture of mature females in the fisheries but almost no

records contain any information on whether the eggs were found in the oviduct, the only sure indication of mature, ready to spawn, females.

According to Squires (1957) *Illex illecebrosus* spawns in December through March but no spawning sites of *Illex* have ever been reported unless an aggregation off the Florida coast in about 1 000 metres was a spawning event. An egg mass was spawned in an aquarium (O'Dor and Durward, 1978) but the major spawning areas are unknown. *Todaropsis eblanae* and *Todarodes sagittatus* in the Mediterranean spawn in December to March and September to November respectively, based upon supposed mature females (Mangold, 1963).

Todarodes pacificus apparently has at least two and possibly three spawning periods. Joo Youl Lim (1967) stated that *T. pacificus* spawns from July to November in Korean waters while Kasahara *et al.* (1969) stated that there are two spawning periods in Japan, winter and summer; these yield three populations. While the spawning times are well known, the actual spawning areas and distribution of eggs have yet to be delimited. *T. pacificus* has been studied biologically from the fisheries standpoint more than any other oceanic squid (Okutani, 1977) but many questions remain to be answered.

Of the three species of *Ommastrephes*, only *O. bartrami* has been studied biologically. Araya (this volume) believes, based upon mature females in the catch, that it spawns in January through May in the warm Pacific waters. They are thought to breed and spawn in deep water. Little is known of their biology in the Atlantic. Hixon *et al.* (1981) have provided some information on *O. pteropus* in the Gulf of Mexico, especially related to fecundity. Ehrhardt *et al.* (this volume) reported upon the biology of *Dosidicus gigas*. According to them it spawns during early winter both in the Gulf of California and along the slope on the western edge of Baja California but data are lacking on spawning grounds, egg clusters and eggs. According to Potter, Winstanley & Caton (this volume) *Nototodarus sloani gouldi* in the Bass Strait area appears to spawn in winter, summer and fall but spawning areas, eggs and larvae are unknown. It appears from this review that there is little reliable data on any aspect of spawning as far as ommastrephids are concerned.

Our knowledge of these events in octopods is much more reliable. Many species of octopus lay eggs and brood in shallow water where they are available for observation and they are amenable to rearing in aquaria. *Octopus vulgaris* in Europe and in many other areas of the world spawns in summer. The eggs are attached in festoons on the underside of rocks, in caves, large shells and other objects. *Octopus briareus* has its peak spawning during January through March. The eggs are laid in short festoons or rarely in a single layer on the underside of coral slabs, in caves, or empty conch shells, all in shallow water. *Octopus joubini* is a small species and lays few eggs usually in old gastropod or bivalve mollusc shells. Two broods probably occur in South Florida, one in the winter and the other in the summer, but only one brood per year occurs in North Florida (Thomas & Opresko, 1973). *Octopus maya* of the Gulf of Mexico and Campeche spawns during the winter in waters less than twelve feet deep, the eggs attached in festoons on rocks, in dead shells and other hard objects (Solís, 1967).

Recruitment. Recruitment refers to the number of young cephalopods entering the fisheries each year as a result of the last spawning season. In a species with a life span of one year, a constant and rather high recruitment is necessary to maintain the stocks against fishing and predation mortality.

Recruitment in the squid fishery is determined by analyzing the length frequency modes in the catch and noting the numbers and times of young squid entering the fishery. In a fishery conducted by jigging, the size of the recruits caught is determined by the catch characteristics of the commercial jigs; small animals are unable to take the jig. Similarly in the trawl fishery the size of the animals caught is determined by the mesh size. Thus the size available for recruitment determination is limited.

In finfish fisheries, the recruitment is determined, in many cases, long before the young show up in the catch and thus there is a predictive capability. Squid eggs, larvae, and early

juveniles are seldom taken by any means and apparently never in sufficient quantities to have a predictive value. As the life span is so short in many species, this lack may not affect fisheries management to any great degree. Most of the commercial species of squid have a high fecundity and, unless there is heavy overfishing or a strong ecological perturbation, they should maintain themselves.

It is probable that little progress can be made in stock predictions and early recruitment figures until more is learned about the areas and times of spawning and the depth levels sought by the hatchlings and early juveniles. Obviously nets are available to catch them if their whereabouts were known. Much more exploratory work is needed in this area of squid research.

Migrations. It is well known that some squid migrate but it is less known that octopods do also. Rees (1952) and Rees and Lumby (1954) have reported upon *Eledone cirrhosa* 'invasions' of the English coast and the sighting of octopus swimming in assumed migrations. Octopus also have a winter/summer movement inshore and offshore in relation to changing water temperatures.

The situation with regard to squid is of a more classical nature. It has long been known that *Todarodes pacificus* migrates in Japanese waters (Okutani, 1977). Squires (1957) described the inshore feeding migrations of *Illex illecebrosus* in Newfoundland waters in summer and fall but the other end of the migration is not known although it may be a southward movement as far as Florida. In the loliginids Tinbergen & Verwey (1945) described a seasonal migration of *Loligo vulgaris* on the Dutch coast while Holme (1974) demonstrated a migration along the British Isles for *L. forbesi. Loligo opalescens* has inshore spawning migrations and aggregations along the California coast but offshore and longitudinal movements have not been noted (Fields, 1965).

There is little information on the movements of most squid and in some cases disappearance in one area and abundance in another may be due to migrations or to long term ecological changes or they may reflect local population fluctuations. *Dosidicus gigas*, long abundant on the Chilean coast as far south as Concepción, practically disappeared from Chile for the last 15 years (Gallardo, pers. comm.) only to become abundant off northern Mexico and in the Gulf of California. In 1982 the species appears to have moved southward and has practically disappeared from the Gulf of California (Ehrhardt, pers. comm.).

The causes of migrations are multiple, including mating and spawning, feeding, seasonal temperature changes, and others. Unfortunately in most species the fisheries are not carried out year round with the vessels following the squid movements. Thus knowledge of the total migratory patterns for most species is fragmentary both in space and time.

Populations. Little is known concerning populations except for a few species and most of the information deals with seasonal populations rather than geographical ones. Verrill (1882) apparently noted population differences when he described several varieties of *Loligo pealei*. Mullin (pers. comm.) noted that the populations of *L. pealei* seemed to change seasonally off the Maryland coast and investigations indicated differences in sucker dentition on the tentacular clubs. Studies of *Lolliguncula brevis* (Voss, unpubl.) showed that stocks could be distinguished on the Georgia/Florida shelf, South Florida, and the Gulf of Mexico by multiple character indices, especially fin size.

Most population distinctions are based upon the times of spawning and appearance of the recruits in the stocks. Holme (1974) thought there were winter and summer spawning populations for *Loligo forbesi* in British waters. Okutani (1977) has reviewed the summer and winter populations of *Todarodes pacificus* in Japanese waters. Seasonal populations are less well documented for other species but data are accumulating that shortly may be useful in distinguishing populations in other species.

Seasonal populations may not be as important from a fishery management viewpoint as are geographical ones but the latter are much more difficult to recognize. It seems unlikely from a longitudinal distribution viewpoint that *Loligo pealei* on the American Atlantic coast and *L.*

opalescens on the Pacific coast should each belong to a single population. This is especially true for *L. pealei* where semibarriers occur at such points as Cape Hatteras and south Florida; nonetheless separate populations have not been discriminated. Along the west coast of North America no apparent barriers exist and *L. opalescens* is found from western Canada to Baja California, a range of approximately 1 500 miles. Various techniques have been used in an attempt to identify populations of this species: morphological characters (Kashiwada and Recksiek, 1978), biochemical-genetic studies (Ally and Keck, 1978), and protein electrophoresis (Christoffersen *et al.*, 1978) but no definite conclusions on the recognition of populations could be reached by any of these methods. Existence of populations, however, seems possible and more extensive studies may well provide answers to these perplexing questions. For the time being the greatest possibility of success seems to lie in detailed morphological studies of characters and combinations of characters showing geographical variation.

The same problems apply to the octopods. Thomas & Opresko (1973) believed that there were summer and winter populations of *Octopus joubini*, which has a short life span. Seasonal populations may be a widespread phenomenon in temperate and cold water species but in strictly tropical waters seasonal populations probably do not occur because of the long duration of spawning or year round spawning.

Population fluctuations of various species of squids and octopuses have been well documented but despite this, normal fluctuations are often misinterpreted as representing changes due to fishing pressure or other factors. The decline of the catch of *Todarodes pacificus* in recent years was considered to be due to overfishing (Okutani, pers. comm.) but in 1980-81 the population rose significantly, leading some biologists to consider that this was a natural population fluctuation or cycle. Fields (1965) showed population fluctuations in *Loligo opalescens* on about a 15 year cycle. Squires (1957) analyzed data on *Illex illecebrosus* in Newfoundland waters and found strong fluctuations in abundance but no definite cyclic pattern.

Prey/Predator Relationships. Cephalopods are active, top level predators. They feed upon numerous invertebrates, especially crustaceans, and many species of fishes, as well as other cephalopods. Cephalopods, in turn, are eaten by large fishes, marine mammals, and many sea birds, forming a large percentage of their diet. Clarke (1962) pioneered the study of mammal predation on cephalopods using the characters of the indigestible chitinous beaks for identification and squid biomass, relating beak size to body size. Much information is now accruing from the identification of cephalopod beaks in whale (Clarke, 1980), fish, and bird stomachs although in many instances identification can be taken only to genus or even family, with a few unknowns even at this level. These hard parts are retained for a sufficient time that a rather accurate estimate may be obtained of the percentage of squids eaten in comparison with other groups of prey animals. Nearly every species of large fish and marine mammal eat squid and the pressure upon the stocks of squid must be formidable (Clarke, this volume).

The major predators upon cephalopods, however, have been greatly reduced as a result of the whale fisheries, depletion of the fur seals, and the heavy inroads upon the large fishes as a result of the high seas longlining and the tuna fisheries. Toll & Hess (1982) have studied the diet of the swordfish in Florida waters where *Illex* spp. constitute over 90 per cent of their diet. Voss (1953) showed that nearly 17% of the diet of sailfish consisted of mixed cephalopods. The result of the depletion of these fishes and others may have resulted in a dramatic increase in available cephalopod stocks. Voss (1973) based part of the estimates of cephalopod resources on data derived from squid consumption by large predators.

Squid predation is much less understood. Cephalopod workers have been remiss in studying stomach contents. The general picture that emerges, however, is that young and small adult squid feed primarily upon small crustaceans: amphipods, copepods, euphausiids, mysids, cumaceans, ostracods, and others, and larval stages of larger crustaceans. As the squid grow there is a move toward larger prey such as other squid and fishes. In large squid the prey

may become almost exclusively squid and fishes. The stomach contents of a giant squid *Architeuthis* taken off South Africa contained only remains of large squid (Peréz-Gándaras & Guerra, 1978).

The most detailed study of the position of a species of squid in a food web was carried out at Moss Landing, California, on *Loligo opalescens*. Karpov and Cailliet (1978) studied the stomach contents of *L. opalescens* from various areas and times of day. They found that this rather small squid fed mainly upon crustaceans throughout its life cycle and even as adults, fishes and squid formed a minor part of their diet. Morejohn, Harvey & Krasnow (1978) examined the gastrointestinal and stomach contents of 1 928 fishes of 86 species and 33 families, 513 sea birds of 28 species and eight families, and 143 marine mammals of 15 species and eight families. On the basis of these two studies the latter writers gave several depictions of the complicated food web of this squid. While these studies can be used for management purposes in California, they cannot be used for the oceanic squids that attain much larger sizes and do not compare with our knowledge of the prey/predator relationships of other species of *Loligo*.

Obviously we know very little concerning the position of squid in oceanic food webs and if squid stocks are to be subjected to heavy fishing pressures such data are needed in order to avoid causing major perturbations in stocks of other groups.

Conclusions

With this review of fisheries biology it becomes readily apparent that few, if any, species of cephalopods have been studied sufficiently to yield information needed for proper management. At least some data are available for the following cephalopods. For others, information is either sparse or lacking altogether.

Eastern Atlantic

Illex illecebrosus coindeti, Todarodes sagittatus, Loligo forbesi, L. vulgaris, Sepia officinalis, Octopus vulgaris, Eledone cirrhosa, E. moschata.

Western Atlantic

Loligo pealei, Doryteuthis plei, Illex illecebrosus, Octopus briareus, O. joubini, O. maya.

Eastern Pacific

Loligo opalescens, Dosidicus gigas, Octopus dofleini.

Indo-West Pacific

Loligo edulis, Doryteuthis bleekeri, Todarodes pacificus, Nototodarus sloani, Symplectoteuthis oualaniensis, Ommastrephes bartrami, Onychoteuthis borealijaponicus, Octopus dofleini, O. cyanea.

It is apparent that of approximately 650 species of cephalopods, there are some management data for only 23 species or about four per cent, some of which have no commercial value. This is only a small fraction of the total number of actual or potential economic species of cephalopods attaining a figure of perhaps 150 species. It should be pointed out that this information is only for restricted areas of the species range and in widely distributed species populational data for one region may not be applicable for another. It is certainly true that data obtained for one species of cephalopod may have little or no value when applied to another.

The biology of no species of cephalopod is as well known as that of almost any commercially exploited fin fish. One only has to look at the wealth of knowledge about cod, hake, sole, halibut, herring, mackerel, anchovies and dozens of others to realize the inadequacy of cephalopod data. Our information on the ecological factors controlling squid distribution and abundance is even more inadequate.

Present cephalopod fisheries practices are based upon the concept that squid live for one year only. While this broad generalization does fit some species, examination of the data given above shows that life spans vary in known species from 4 months to 4 years and accurate knowledge of the life span of heavily fished oceanic squid is still lacking. Similarly, fecundity figures are so widely varying in the same species between different authors that present figures are unconvincing.

More ship time and laboratory research has

been expended on plankton studies than any other phase of marine biological work. Yet few cephalopod eggs have been obtained and larvae are sparse. For most oceanic species spawned eggs are unknown and larvae undescribed. Surely these fundamental phases of cephalopod life cycles could be uncovered with adequate funding, a fair share of ship time, and properly planned research programs.

At present we are at a complete loss to explain the questions of squid disappearance from an area for years only to reappear in almost original numbers as occurred with *Todarodes pacificus* in Japan with drastic effects upon the world squid market. Similarly *Dosidicus gigas* appeared and disappeared in the Gulf of California. Thus a promising new fishery was developed and left stranded. Even seasonal movements are unknown for most species simply because research ships are not involved except when the fishery is in operation. Millions of dollars have been spent on seeking the pathways and spawning grounds of the European and American eels with little foreseeable impact upon either the eels or their fisheries. How much has been spent to track squid migrations and discover squid spawning grounds other than in Japanese waters?

From a fisheries viewpoint can we afford to gamble on investments in ships, gear and men at a time when foreign vessels are being more and more restricted from national waters? The time seems to be approaching when, if a national fishery fails, ships cannot move to another country to exploit new stocks. This is as much a political problem as it is a biological one.

This review makes it clear that much more attention must be paid to the biological factors. While mathematical models based upon catch figures may suffice for management of a healthy fisheries, they do not show the causes of declines based upon other than overfishing. Real figures are required, derived from knowledge of the biology of the species exploited.

The cephalopod fishery today amounts to about 1.3 million metric tons. Its potential on the continental shelf alone is estimated at between 7-10 million metric tons. It is perhaps the largest source of harvestable but underexploited protein in the oceans. Yet the amount of money expended in biological research on our squid fisheries on a worldwide basis is not as large as that expended on the study of only one family of pelagic fishes alone, the Scombridae. Surely cephalopod fisheries biology deserves better treatment from the hands of the fishery services of the world.

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There is a very large and diverse literature dealing with cephalopod biology. Much of it is in obscure journals, widely ranging fisheries sources, and often in languages difficult for workers of western European origin. Leads to much of this, however, may be obtained through searching the bibliographies in the following sources. A full bibliography of cephalopod fisheries papers is much to be desired.

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AUSTRALIAN CEPHALOPOD RESOURCES

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Abstract

Australian domestic catches of cephalopods total less than 1000 tonnes per annum and comprise many species none of which is intensively fished as a target species except in extremely localised situations. Recent catches by foreign fishing vessels operating within the 200-mile Australian Fishing Zone have shown that large squid and cuttlefish stocks occur in tropical waters off northern Australia and large squid stocks occur in temperate waters off southern Australia. Modest improvements in local markets and increased local awareness of these and other cephalopod resources have led to an upsurge in experimental and exploratory fishing and biological studies.

This paper summarises the fragmentary information on the occurrence, fisheries and biology of exploited and commercially potential cephalopod resources in Australian waters.

Introduction

This paper provides an overview of the exploited Australian cephalopod resources, including a summary of the biology of species for which information is available. A number of species with potential for exploitation have also been included.

Australian cephalopod fisheries are small—the domestic catch was less than 1,000 tonnes in 1979/80—and fisheries for many species are in their infancy. Until recently most cephalopods taken by Australian fishermen were destined for the bait market. While this remains important, the proportion of squid caught for human consumption has increased considerably during the last decade. Annual consumption of squid in Australia now exceeds 2,600 tonnes, but some 70 per cent of this is imported, mostly as frozen squid tubes from south-east Asia (Anon., 1980f).

Catches by foreign fishing vessels operating in and adjacent to the 200-mile Australian Fishing Zone (AFZ) have overshadowed domestic catches in recent years. Squid jigging vessels took 3387 and 7914 tonnes of squid from south-east Australian waters in 1978/79 and 1979/80, respectively. The cuttlefish component of the catch of Taiwanese pair trawlers operating in north and north-west Australian waters is of the order of 600 tonnes annually (Demersal Fisheries Research Centre 1980). Squid is the most important component in the catches by Taiwanese pair trawlers operating in the Arafura and Timor Seas (Liu *et al.*, 1978) with a total catch of 2660 tonnes in 1979 (Demersal Fisheries Research Center 1980). However, the AFZ database (based on logbook information from feasibility and licensed foreign fishing vessels) shows that in 1980, Taiwanese pair trawlers caught a total of only 370 tonnes of squid within the AFZ.

These figures indicate that although exploitation by Australian vessels is light, there are significant squid resources in Australian waters. As a consequence of low domestic catches, until recently, investigations of squid and other cephalopod resources have been accorded relatively low priority by Australian fisheries agencies. Hence there is little published information available on most cephalopod species in Australian waters.

In this paper the available information for each species is summarised under three headings:

(i) distribution, including geographic range in Australian waters, depth range, position in water column and seasonal and diurnal variations in occurrence;
(ii) biology including fisheries biology;
(iii) exploitation including experimental fishing results.

Reference is made to ongoing studies under the appropriate sections.

No attempt is made to compare results of local studies with those of overseas work on similar species or to summarise overseas infor-

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mation for a species when there is none for that species in local waters.

Order TEUTHOIDEA, Family LOLIGINIDAE

Members of this family are neritic or continental shelf-dwelling species. Larger species are generally of commercial value.

Four species are already exploited by Australian fishermen and are described in more detail below. Several other species have been collected in northern Australian waters, but there is very little information on their distribution and abundance. They include commercially valuable species such as *Loligo edulis* Hoyle and *Doryteuthis singhalensis* Ortman.

Loligo chinensis Gray, 1849

Distribution: L. chinensis is synonymous with *L. etheridgei*, *L. formosana* and *L. indica* (Natsukari & Okutani, 1975) and occurs in the waters off Taiwan and southern China, the Gulf of Thailand, Arafura Sea and tropical and subtropical Australian waters (Tomiyama & Hibiya, 1978); it is also widely distributed off south-eastern Australia (Macpherson & Gabriel, 1962). It inhabits the shallow waters of the continental shelf and coastal bays and inlets (e.g. Gorman & Graham, 1981b). Off the coast of southern Queensland a few specimens have been taken by jig in waters as deep as 300 m (Potter, unpubl. data).

Biology: In southern Queensland waters *L. chinensis* grows larger than 600 g and 38 cm mantle length (ML). However, males and females mature as small as 12 cm ML and mature specimens can be found in most months (Potter, unpubl. data). *L. chinensis* exhibits a behavioural characteristic observed in other loliginids (Serchuk & Rathjen, 1974), congregating near the sea floor during the day and rising in the water column after dark. Consequently, demersal trawl catches are greater during daylight hours.

The seasonal abundance and reproductive biology of *L. chinensis* in southern Queensland is currently being investigated, but there is no published information yet available.

Exploitation: Most of the domestic catch of *L. chinensis* is taken as a by-catch of prawn trawling. However, this species becomes a target species at certain times of the year in some areas such as Moreton Bay, Queensland, where the maximum size commonly trawled is about 18 cm ML and the minimum size retained is approximately 7 cm ML. Larger specimens are occasionally taken by recreational fishermen on baited jigs or lures.

Landings of this species in Moreton Bay are highest in May but the quantities landed are strongly influenced by prawn catches and squid prices, and the local markets for squid can easily become saturated causing a decline in squid landings. When prawn catches are poor, fishermen trawl for *L. chinensis* as an alternative target species. Consequently the stocks of *L. chinensis* in Moreton Bay are not considered to be fully exploited (Potter, pers. obs.).

The species composition for the squid catch taken by Taiwanese pair trawlers operating in northern Australian waters is not known. However, *L. chinensis* is known to be abundant in parts of the Gulf of Carpentaria and Torres Strait and it is believed that this species might be an important component of Taiwanese pair trawl catches in the Arafura Sea area. Total squid catches in this area in 1976 were assessed as 17 per cent of a total catch of 44,900 tonnes (Liu *et al.*, 1978) and the same authors considered that less than 10 per cent of the potential yield (for all species) is being taken from the Arafura Sea. Much of this area, however, lies outside the declared AFZ. The recorded catch within the AFZ in 1980 was only 370 tonnes (AFZ database).

Loliolus sp.

Distribution: This species is presently being described (C. C. Lu, pers. comm.). It occurs in shallow coastal and estuarine waters on the east coast of Australia from northern Queensland to southern Victoria. Specimens have been collected in rivers and creeks with salinities as low as 2.2 per cent (Potter, unpubl. data).

Biology: No published information.

Exploitation: This species is caught incidentally by prawn trawlers and because of its small size (<8 cm ML) is usually marketed in Queensland and New South Wales as bait (Potter, pers. obs.).

Sepioteuthis australis Quoy and Gaimard, 1832

Distribution: Southern calamary *S. australis* occurs in coastal waters, bays and inlets of southern Australia from southern Western Australia to New South Wales. It is usually caught in depths less than 70 m and although its occurrence in research and commercial catches suggests that it is a largely demersal species (i.e. it is seldom trolled or caught by jigging machines) it is often observed at the surface (Gorman & Graham, 1981a,c).

Biology: During late winter and spring, clusters of eggs have been found attached to algae on reefs and to seagrasses in Port Phillip Bay, Western Port and Portland Bay, Victoria (Winstanley, unpubl.). Observations in South Australian gulfs show that several females may deposit eggs in collective egg-masses attached to seagrass, ascidians and other benthic organisms at depths of 3-20 m (Smith, 1981a).

Field and aquarium studies of the biology of *S. australis* are in progress in South Australia (Smith, 1981a).

Exploitation: S. australis is caught incidentally in bays and estuaries in seine nets, gill nets and prawn trawls and, in coastal waters, in fish and prawn trawls and Danish seines. During some seasons in gulfs and bays it is the target species for commercial fishing with seine nets and baited jigs on handlines. For instance, inside the entrances to Port Phillip Bay and Western Port, Victoria, both methods are used to take *S. australis* mainly in spring; smaller catches are taken in autumn mainly in seine nets. The annual catch is in the order of 100 tonnes (Winstanley, unpubl. data). In South Australia most of the catch in autumn and winter (the most productive seasons) is taken with seine nets and most of the catch in spring and summer is taken with handlines. The 1979/80 catch was 193 tonnes (Smith, 1981b).

Sepioteuthis lessoniana Lesson, 1830

Distribution: Northern calamary, *S. lessoniana*, is widely distributed throughout the Indo-Pacific from Japan to Australia and Hawaii to the east coast of Africa (Voss & Williamson, 1971). In Australian waters it inhabits subtropical coastal waters, bays and inlets from depths of less than 1 m to in excess of 100 m.

Biology: In Moreton Bay, Queensland, eggs were obtained in September from artificial collectors in shallow water (1-3 m), and hatching commenced after approximately 35 days at 20-24°C (Potter, unpubl. data).

Exploitation: S. lessoniana is taken for human consumption. In southern Queensland it is a prime market species taken mainly by tunnel net fishermen operating in the intertidal zone in Moreton Bay and Great Sandy Strait, from April to October. Prawn trawlers operating on the continental shelf in the same region take incidental catches during the same period. In the last few years handline fishing with baited jigs and lures from bayside jetties has become more popular, but this is still a small fishery (Potter, pers. obs.).

Order TEUTHOIDEA, Family OMMASTREPHIDAE

This family comprises neritic and oceanic species: *Nototodarus gouldi* (McCoy, 1888) is the major commercial species off south-eastern Australia; *Ommastrephes bartrami* (Lesueur, 1821) and *Symplectoteuthis oualaniensis* (Lesson, 1830) both of which are commercially exploited elsewhere in the Indo-Pacific, occur in offshore waters of the AFZ (Clarke, 1966; Nesis, 1979; Dunning *et al.*, 1981) and *Todarodes filippovae* Adam, 1975 occurs in the Southern Ocean and along the southern Australian coast (Anon., 1978, 1980c; Okutani, 1980) and might represent a latent resource (Okutani, 1980).

Nototodarus gouldi (McCoy)

Distribution: Gould's squid *N. gouldi* occurs in continental shelf waters off southern Australia from Queensland to Western Australia. Although it is sometimes abundant in shallow coastal waters and estuaries, particularly in summer, the greatest numbers occur in waters 50-200 m deep. The species has been trawled from as deep as 640-825 m in the Great Australian Bight (Berry, 1918) and as deep as 485 m off New South Wales (Gorman & Graham, 1981a). Schooling behaviour and the apparent occurrence of distinct broods (see below) contribute towards the variability in

distribution and abundance with locality and season (Anon., 1978, 1980c; Harrison, in prep.).

Biology: N. gouldi regularly grows to sizes of 1200 g and 40 cm ML and females grow to larger sizes than males (Anon., 1980c).

Several size-classes of squid are present in the Bass Strait region (Anon., 1978, 1980c; O'Sullivan, 1980a; Harrison, 1979, in prep.), possibly resulting from discrete spawnings or from variable mortality of larvae and juveniles (Harrison, in prep.). The summer spawning season can be clearly defined as in 1978/79 (January-February), or indistinct as in 1979/80 (December-March) (Harrison, in prep.).

According to Harrison (*op. cit.*), during the December-April fishing season in Bass Strait, jig catches comprise: remnants of the previous autumn brood mainly in December; a late winter or spring brood, the bulk of the catch; and a summer brood, mainly in March and April.

From catch data, Harrison (in prep.) estimated that the Bass Strait spring brood in 1979/80 grew at monthly rates that varied with locality from 109 to 200 g/month. Using the mantle length-weight relationship

$$W = 0.0183\mathrm{ML}^{3.1073}\ \mathrm{kg}$$

together with monthly modal weights he found that the relationship

$$W = 1.06\ [1\text{-}2^{-0.3(t+1)}]^3\ \mathrm{kg}\ (t \text{ in months})$$

provided a useful approximation to growth during the summer-autumn fishing season. Smith (1983) calculated a similar length-weight relationship for *N. gouldi* off Victoria and South Australia in 1979/80. From studies of modal progressions, growth of 1-2 cm/month has been reported from this region (Anon., 1978; Smith, 1981a). Harrison (in prep.) considered that *N. gouldi* lives no more than one year, however there are no data on longevity.

Off south-eastern Australia between September and April most males and females bigger than 22 cm and 30 cm ML, respectively, are sexually mature (Anon., 1978, 1980c, 1980e). But off New South Wales most females bigger than 22 cm ML are mature and copulated (Gorman & Graham, 1981a, b). The male produces up to several hundred spermatophores and, during mating, transfers these into the female's buccal pouch where fertilisation occurs subsequently (Harrison, in prep.); the time elapsing between mating and fertilisation is not known.

O'Sullivan (1980a, b) showed that *N. gouldi* is an opportunistic predator feeding on planktonic crustaceans, fishes and cephalopods. As squid grow, the incidence of crustaceans in the diet decreases while the incidence of cephalopods (including *N. gouldi*) increases. Feeding occurs mainly at night and at dawn, and food passes through the digestive tract rapidly.

Predators include seals, dolphins, tunas and benthic and bathypelagic fishes, notably school shark *Galeorhinus australis* (Macleay) (Olsen, 1954). In a study of the diets of 52 fish species exploited off Victoria, Coleman and Hobday (1982) found *N. gouldi* in the diets of only eight species with the greatest occurrence of 4-6 per cent in school shark and gummy shark *Mustelus antarcticus* Gunther. They suggested that increased exploitation of squid off Victoria would be unlikely to adversely affect fin-fish populations.

Echosoundings and trawl catches indicate that *N. gouldi* congregates close to the sea floor during the day and disperses into the mid and surface waters during the night. Limited tagging studies off south-eastern Australia have shown some movements in the order of 60 n.mi. (3 days) but recapture data are too few to show systematic movements of squid schools (Anon., 1980c).

Using catch and effort data from fishing logs of feasibility fishing boats in eastern Tasmanian and Bass Strait waters, Harrison (in prep.) estimated growth parameters, catchability coefficients; total, fishing and natural mortality rates; initial population size; yields and optimum levels under various combinations of parameter values. Natural mortality (M) appeared to increase sharply about 100 days after the start of the fishing season. This increase appears to coincide with the onset of spawning. Cannibalism is suggested as a significant component of M during the first 100 days although there is no direct evidence of this.

With some exceptions or ambiguous observations, squid catch rates have usually been found to be lowest in the full moon period (Anon., 1980c, 1980d; Gorman & Graham, 1981a; Smith, 1981a).

In comparing catch rates during the seasons from 1977/78 to 1980/81, the low rates obtained in 1979/80 have been ascribed to unusual oceanographic conditions in Bass Strait characterised by the absence of a marked thermocline (Anon., 1980e; Caton, 1981), and slightly lower maximum temperatures than in the two earlier seasons (Anon., 1980e; Harrison, in prep.). Commercial catch rates are obtained in waters ranging in temperature from 14° to 18°C (Anon., 1978).

In January-March 1980 in the Great Australian Bight, demersal trawls in the depth range 95-830 m showed that *N. gouldi* was most abundant in waters 300-400 m deep, occurred in 96 per cent of all hauls at these depths and were mainly caught during the day. In waters off South Australia, and off western and southern Tasmania the species occurred in about 50 per cent of all demersal and pelagic trawls where surface temperatures were between 12° and 24°C but were most abundant where surface temperatures were between 18° and 22°C (Collins & Baron, 1981).

During the 1980/81 season in Bass Strait and off western Victoria, comparisons were made of catch rates, length frequencies and sex ratios by fishing method (automatic and hand jigging), time of day and bottom depth (Anon., 1981c). Results showed that:

(i) catch rates for females were higher than for males using both fishing techniques;
(ii) catch rates by jigging machine increased progressively through the night while those from hand jigging were fairly constant;
(iii) mean lengths of machine-jigged squid decreased during the night while those of hand-jigged squid were constant;
(iv) hand-jigged females were larger than males while machine-jigged males and females were of similar sizes;
(v) hand-jigged squid were larger than machine-jigged squid; and
(vi) squid were caught at low rates in daylight hours.

Analysis of feasibility fishing results (T. I. Walker, unpubl. data) showed that catch rates exceeded 1 tonne per night where surface temperatures were 14°-19°C (range studied 11°-20°C) and that catches were greatest at depths of 40-100 m. Kowarsky and Mobley (1982) confirmed some of the observations (i)-(vi) above.

Exploitation: With few exceptions most commercial landings of *N. gouldi* by Australian fishermen have resulted from incidental catches during demersal trawling or trolling operations. A notable exception occurred during the summer of 1972/73 in the Derwent River estuary, Tasmania, where large numbers of squid appeared and 154 tonnes were caught by boats fitted with improvised gear (Wolfe, 1972). The order of magnitude of these domestic squid landings from New South Wales, Victoria, Tasmania and South Australia is 200 tonnes annually. Most of this is caught by trawlers in New South Wales offshore waters whence reported catches of all squid (mainly *N. gouldi*) have increased from 19 tonnes in 1975/76 (Anon., 1977) to 110 tonnes in 1978/79 (Anon., 1981b).

Squid feasibility fishing conducted during 1978/79 and 1979/80 (AFZ database) showed that the magnitude of squid catches taken by jigging off south-eastern Australia might be increased to several thousand tonnes annually. In 1978/79, 19 vessels caught 3,387 tonnes from December to May, mainly in the waters off western Victoria, western Bass Strait and eastern Tasmania. During the same period of the following year, 64 vessels fished over a wider area including eastern Victoria and South Australia and caught a total of 7,914 tonnes of squid. Western Bass Strait and northern Tasmanian waters were the most productive. Feasibility fishing was also conducted off south-western Western Australia during 1979/80 by a fleet of 22 vessels. Their catch was disappointingly low (808 tonnes) in contrast to catches from south-eastern Australia.

Feasibility fishing ended in 1979/80 and because of depressed world markets for squid,

joint venture operations have not proceeded since then.

Between October and March from 1977/78 to 1980/81 a Japanese squid research vessel fitted with jigging machines conducted resource surveys and biological studies of *N. gouldi* mainly in Tasmanian and Bass Strait waters. In the last year, operations were also conducted in South Australian, Victorian, and southern Queensland waters. Catches of 46, 121, 44, and just over 80 tonnes of *N. gouldi* were taken in those successive seasons, respectively (Anon., 1978, 1980c, 1980e; Caton, 1981). These catches are not directly comparable because of differences in the amounts and localities of fishing.

Australian vessels' attempts at midwater trawling and bottom pair-trawling for *N. gouldi* have been unsuccessful (Caton, 1981). Surface, subsurface and bottom mesh netting in Bass Strait has also been unsuccessful, leading to the conclusion that mesh netting is not an appropriate fishing method for this species (Jameson, 1981).

Ommastrephes bartrami (Lesueur, 1821)

Distribution: O. bartrami, a large oceanic species known as red ocean squid, occurs in subtropical waters of the southern Pacific and in the north-western Pacific (Collins & Dunning, 1981). It has been taken in research cruises and by commercial vessels off southern Western Australia (M. Dunning, pers. comm.), in the Great Australian Bight, in eastern Bass Strait, off New South Wales (Gorman & Graham, 1981a), and off Queensland as far north as 23°42′S (Dunning *et al.*, 1981). At all of these localities it has been caught in the deeper waters of the continental shelf and beyond.

Biology: No published information for Australian waters.

Exploitation: This species is presently not exploited in Australian waters.

In April 1981 a commercial fishing boat chartered for experimental squid mesh netting caught almost 290 kg of *O. bartrami* off north-eastern Tasmania and in eastern Bass Strait (Jameson, 1981). This species was found to be better suited to capture by mesh netting than the intended target species, *N. gouldi*, and further fishing was conducted during 1982 (Anon., 1982).

Also in April 1981 the Japanese research vessel *Hoyo Maru 81* caught more than 300 kg of *O. bartrami* weighing between 100 and 3000 g using automatic jigging machines in waters more than 1000 m deep off north-eastern Tasmania. Smaller catches were also taken east of Flinders Island and in deep water off eastern Bass Strait. Later in the month catches of *O. bartrami* were taken off southern Queensland (Dunning *et al.*, 1981).

Symplectoteuthis oualaniensis (Lesson, 1830)

Distribution: S. oualaniensis is widely distributed throughout tropical oceanic waters of the Indo-Pacific from the west coast of Central America to the Cape of Good Hope and from southern Japan to Australia (Tomiyama & Hibiya, 1978).

Biology: There is no published information for Australian waters.

Exploitation: This species is exploited commercially off the Ryukyu Islands of southern Japan and off Taiwan (Okutani & Tung, 1978). It is not exploited in Australian waters but small catches were taken during a cruise of the Japanese research vessel *Hoyo Maru 81* off southern Queensland in April 1981 (Dunning *et al.*, 1981). There is no other published information on this species in Australian waters.

Order SEPIOIDEA, Family SEPIIDAE

The Australian cuttlefish fauna appears to be the richest in endemic species in the world with about 20 species (Adam & Rees, 1966; Adam 1979) but exploitation of the resources by Australian fishermen is low. A number of these species may have some potential for future exploitation if suitable export markets are developed.

Sepia pharaonis Ehrenberg, 1831

Distribution: S. pharaonis is distributed throughout the Indo-West Pacific region from the Red Sea to southern Japan. In Australian waters it occurs from Rottnest Island (Western Australia) through northern Australian waters to the Capricorn Group at the southern end of

the Great Barrier Reef (Queensland) (Adam, 1979).

Biology: There is no information available on the biology of this species in Australian waters. It is amongst the largest of the cuttlefish growing to 4 kg in weight (Tomiyama & Hibiya, 1978).

Exploitation: This cuttlefish is widely exploited by trawlers operating off the Arabian Peninsula (Okutani, 1977) and in south-east Asia (Tomiyama & Hibiya, 1978). Taiwanese pair trawlers caught approximately 600 tonnes of cuttlefish off northern Australia in 1979 (Demersal Fisheries Research Center 1980). The catch reported from within the AFZ was about 350 tonnes in 1980 (AFZ database). Approximately 90 per cent of this cuttlefish catch was *S. pharaonis* (C. C. Lu, pers. comm.).

Small quantities of this cuttlefish, caught incidentally by prawn trawlers, are occasionally sold in local markets on the east coast of Queensland (Potter, pers. obs.).

Other **Sepia** species

Distribution: Off southern Australia two *Sepia* species, *S. apama* Gray and *S. braggi* Verco are exploited commercially (Winstanley, 1981, unpubl. data). *S. apama* is the largest and most abundant and occurs over reefs, seagrass beds and open trawl ground in coastal waters and bays.

In subtropical and tropical waters a number of species are occasionally marketed including *S. chirotrema* Berry, *S. rex* Iredale and *S. elliptica* Hoyle (Potter, pers. obs.).

Biology: No published information.

Exploitation: New South Wales cuttlefish landings, mainly by trawlers, have risen from 17 tonnes in 1975/76 to 87 tonnes in 1978/79 (Anon., 1981b). Small quantities of cuttlefish are landed in other states, taken incidentally in trawls, beach seines and fish traps.

Order OCTOPODA, Family OCTOPODIDAE

Octopus in Australian waters have only been lightly exploited.

Considerable interest has been developing in recent years in the market possibilities for octopus taken incidentally in rock lobster pots and some research has been directed to investigating this potential. Domestic markets for octopus are small, but some species are suitable for export particularly to the Japanese market.

Octopus australis Hoyle, 1885

Distribution: O. australis occurs among ascidians, sponges and molluscs and in seagrass beds in bays and coastal waters off southern Australia (Macpherson & Gabriel, 1962, Winstanley, unpubl.).

Biology: Tait (1980) described some aspects of the ecology and life history of *O. australis* in Port Phillip Bay, Victoria. Females brood one group of 50-130 eggs measuring about 11 mm long, mainly during summer. Eggs are usually attached to the inside of an old mud oyster (*Ostrea angasi* Sowerby) shell, a drink can or similar object. After 100+ days the young hatch and immediately adopt a benthic existence. During their lifespan, estimated at 18-20 months, males grow to 210 g and females to 105 g. Once females commence brooding, their food intake diminishes and they usually lose weight. *O. australis* feeds mainly on isopods; the diet also includes other crustaceans, gastropods, bivalves, polychaetes and octopus.

Exploitation: This species is virtually unexploited. Trivial quantities are caught incidentally in scallop and mussel dredging and beach seining operations in Port Phillip Bay. Because of its small size and slender arms it is difficult to skin and is sold mainly for bait. Its main development potential appears to be extremely limited, for instance as bait for the longline fishery for snapper *Chrysophrys auratus* (Bloch and Schneider) (Winstanley & Kearney, 1982).

Experimental trapping in Port Phillip Bay has shown that catch rates of *O. australis* varied with trap type and locality from 0 to 52 octopus per 100 trap-lifts (Winstanley & Kearney, 1982).

Octopus flindersi Cotton, 1932

Distribution: O. flindersi occurs on coastal reefs off South Australia and Western Australia and is prominent as a predator of southern rock lobsters *Jasus novaehollandiae* Holthius especially those trapped in pots (Anon., 1981a).

Biology: No published information (apart from observation of predation on rock lobsters in pots).

Exploitation: South Australian rock lobster fishermen are keen to catch *O. flindersi* mainly to reduce predation on the highly-valued rock lobsters. Trial exports have shown that the large size and toughness of this species make it unacceptable for Japanese markets while the lack of adequate freezer-storage facilities hinders development oriented towards local or European markets (Anon., 1981a). Competition from West African trawled octopus eroded some progress made in marketing in Europe during 1982 (Winstanley, unpubl.).

Octopus pallidus Hoyle, 1885

Distribution: O. pallidus occurs off New South Wales, Victoria, Tasmania and South Australia (Macpherson & Gabriel, 1962). These authors stated that the species is often trapped in rock lobster pots and have been taken in depths as great as 366 m. However, commercial fisheries and research catch information (Winstanley, unpubl. data) suggests that *O. pallidus* is largely confined to depths less than 110 m and occurs mainly among bryzoans, sponges and ascidians suggesting that the above report may have involved misidentification.

Biology: No published information.

Exploitation: Most of the commercial landings of *O. pallidus* (mean size about 500 g) are incidental catches by inshore fish or prawn trawlers and by Danish seiners which also catch small quantities of other *Octopus* species (Winstanley, pers. obs.). The total annual catch of these species from New South Wales and Victorian waters is in the order of 160 tonnes (Anon., 1981b; Winstanley, unpubl. data).

Dix (1981) described the results of an octopus trapping survey conducted off northern Tasmania between November 1980 and August 1981. The total catch of 6.7 tonnes comprised *O. pallidus* (92 per cent, mean weight 810 g) and a larger unidentified species (mean weight 2120 g). Monthly catch rates for *O. pallidus* were highest in April (64 per 100 trap-lifts) and lowest in November (18 per 100 trap-lifts).

During 1981 and 1982, experimental trapping has been conducted in Port Phillip Bay and off the central Victorian coast. At the latter location between August 1981 and May 1982 (in depths of 35-70 m), catch rates were highest in October (44 per 100 trap-lifts) and were low (8-13 per 100 trap-lifts) during other months. During this period the mean size increased to 700 g (Winstanley, unpubl.). In Port Phillip Bay, catch rates varied with locality and trap type from 0 to 10 per 100 trap-lifts in March and April 1982 (Winstanley & Kearney, 1982).

Octopus tetricus Gould, 1852

Distribution: O. tetricus occurs off southern Western Australia and has been reported to occur off eastern Australia (Joll, 1977a). In Western Australia it inhabits coastal reefs where it is a major predator of western rock lobster *Panulirus cygnus* George trapped in pots (Joll, 1977b); it also inhabits seagrass beds such as occur in Cockburn Sound near Fremantle.

Biology: Because of its significance as a rock lobster predator and, more recently, its value as a resource with fishery potential in its own right, *O. tetricus* has been studied more than any other *Octopus* species in Australian waters. In aquaria with excess food available, *O. tetricus* grows rapidly and the daily feeding rate is a function of weight and water temperature; food intake diminishes and weight loss occurs in ageing animals (including brooding females) and there is an approximately linear relationship between growth in weight and daily feeding rate (Joll, 1977a).

Males mature at sizes of 100-150 g and females at larger sizes. After copulation spermatazoa are stored for 12-114 days before egg-laying (usually nocturnal) which occurs over several days. Eggs are laid in strings and a female weighing 2.1 kg laid approximately 150,000 eggs.

Embryonic development varies inversely with water temperatures and takes 22-36 days; hatching of 2.5 mm long larvae takes 6-28 days. During the period of embryonic development and hatching, females cease feeding and actively tend and defend their eggs then die 5-20 days after their eggs have all hatched (Joll, 1976).

Exploitation: Although Joll (1977b) estimated

the annual quantity of octopus (largely *O. tetricus*) caught by rock lobster fishermen as 138-247 tonnes, commercial landings statistics and reports (Anon., 1980b) show that virtually all of this was killed and discarded or used for bait. Experimental trapping and resource assessment work (see below) resulted in an increase in reported landings from 1 tonne in 1978/79 to 29 tonnes in 1979/80. A trial shipment of *O. tetricus* (mean live weight 0.7 kg) showed that, properly processed and frozen, this species is most acceptable to the Japanese market (Anon., 1980a). Kimura (1979) estimated that 30,000 tonnes could be caught annually from Fremantle to north of Geraldton.

Fishery development investigations off southern Western Australia have been conducted in three phases (Anon., 1980a). From March to May 1978, various fishing methods, gear types and localities were tested, then from November 1978 to March 1979, commercial feasibility fishing trials were conducted in Cockburn Sound and off Geraldton resulting in a total catch of 5 tonnes which were processed and shipped to Japan. A detailed account of this second phase of the survey (Kimura, 1979) describes the vessel, gear, methods, export considerations, market evaluations and recommendations for Australian fishermen. From December 1979 to June 1980, a full-scale commercial feasibility trial was conducted using a Japanese octopus-trapping vessel at the same localities using cylindrical traps made of PVC pipe. The results show that catch rates vary within and between seasons with means of 5.44, 9.66 and 5.31 per 100 holes (4 holes per trap) during the three phases. Best results were obtained between January and June (Anon., 1980b).

Octopus species

Distribution: One or more large *Octopus* species of uncertain identity occur on coastal reefs at depths of 0-50 m off south-eastern Australia and are reported to reach sizes of 14 kg (Winstanley, unpubl.). These are similar to *O. flindersi*.

Biology: No published information.

Exploitation: As with *O. tetricus* and *O. flindersi* these species are mainly encountered and exploited by rock lobster fishermen most of whom do not actively seek to catch them. Recently a few South Australian fishermen have experimented with traps or have modified their rock lobster pots to retain octopus and catches of up to 0.5 tonnes of 1-5 kg octopus per month have been reported from a boat fishing in shallow reefs (0-25 m) during summer in Discovery Bay, western Victoria. Low prices on local and European markets have discouraged development of a fishery for these species (Winstanley, unpubl.).

Fishermen do not discriminate between the species of octopus they land so it is difficult to estimate the degree of exploitation for each species. The total annual catch of the above *Octopus* species plus *O. flindersi* off South Australia is in the order of 100 tonnes (Anon., 1981a).

Private and government-funded investigations of capture methods and fishery potential have been conducted by fishermen in south-eastern Australia (e.g. Anon., 1981a, d). The only account of results of such work (Dix, 1981) is discussed under *O. pallidus*.

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PRESENT STATUS OF NORTH AMERICAN SQUID FISHERIES

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Abstract

North American squid resources are not well developed as commercial fisheries. Short-finned Squid, *Illex illecebrosus*, is moderately exploited between Newfoundland and Cape Hatteras in the Northwest Atlantic. Along the east coast of the United States some exploitation of Long-finned Squid, *Loligo pealei* occurs. In California a limited traditional fishery for Market Squid, *Loligo opalescens* is conducted. While in the Gulf of California (Mexico) a fishery for Jumbo Squid *Dosidicus gigas* is developing. Elsewhere a variety of squid resources exists but these are not aggressively sought after at this time.

Traditionally, North American fisheries have not included a strong usage of squids as part of the landings base. One exception is in Newfoundland, Canada, where inshore harvesting of squid has occurred for over a century. The catch consists of *I. illecebrosus*, taken with jigs and used as bait in the cod fisheries of the Grand Bank and adjacent areas. Another exception is on the North American west coast in California, where limited fishing for *L. opalescens* has occurred since at least 1863.

Until recently squid catches off the northeastern United States have been incidental trawl and trap catches, mostly of *L. pealei* with some *I. illecebrosus* occasionally taken.

This situation has changed dramatically in the last decade (Rathjen *et al.*, 1979) with the development of directed fisheries for *L. pealei* along the edge of the northwest Atlantic continental shelf and for *I. illecebrosus* from the Canadian banks to Cape Hatteras. These fisheries, engaged in primarily by foreign fishermen, peaked in 1979 with a production of about 200 000 tons from the northwest Atlantic off Canada and the United States. More than 85 per cent of this total was *Illex*, harvested mainly from Canadian waters. These totals declined in 1980 due to limited market opportunities resulting from high world production (FAO, 1981).

Substantial quantities of squid also are known to exist in the southeastern United States and in the northeast Pacific and Bering Sea. There is very limited development of these resources at the present time. A general discussion of the situation around the perimeter of North America follows.

Northwest Atlantic—Canada

The escalation of *Illex illecebrosus* fisheries in this region has been dramatic, increasing from an average of about 4 700 metric tons for the period from 1970-1974 to over 155 000 tons in 1979 (Lemon & Rycroft, 1982). These squid fisheries have been conducted inshore and offshore with various gears including jigs, traps, and trawls (Hurley, 1980). The peak production in 1979 was a result of increased inshore jig fishing, particularly off Newfoundland (Figure 1).

During the late 1970's a substantial portion of the Canadian production was prepared as a frozen product for shipment to the Japanese markets. Increasing worldwide competition and improved fishing off Japan (Court, 1982) led to a great reduction in these market opportunities during 1980 and 1981 (Raynes, 1982).

Northwest Atlantic—United States

Two squid species of commercial significance are *L. pealei* and *I. illecebrosus*. Both of these species occur off all of the eastern United States but are sought by fishermen only north of Cape Hatteras. *Loligo* concentrates in the winter on the outer edge of the continental shelf from the southern edge of Georges Bank to Cape Hatteras. In the spring, they migrate inshore to spawn, and from May to November are distributed over most of the shelf (Figure 2). *Illex*, the lesser known of the two species, is found over the continental shelf in the summer. North of Cape Cod, *Illex* is the only species regularly found in commercial quantities. Of the two, *Loligo* is the preferred species on the

Figure 1. Portion of small boat fleet at Holyrood at the head of Concepcion Bay, Newfoundland. Here small boats from 4-14 m take Short-finned Squid (*Illex illecebrosus*) using hand operated and automatic jigging reels.
(Photo: W. F. Rathjen)

world market, commanding a price two to three times that of *Illex*.

Trawl fishing along the edge of the continental shelf has been the focus of most of the foreign fishing effort in the U.S. Fishery Conservation Zone. Target species are *Loligo* and *Illex*. *Illex* is trawled on the outer edge of the continental-shelf in the summer. In the late fall, the composition of the squid catch changes, so that by December, catches are almost entirely *Loligo*. The entire catch from this offshore fishery is frozen at sea and consumed in either Europe or Asia. The major countries involved in the fishery in recent years have been Spain, Italy, and Japan (see Table 1).

The major U.S. fishery for *Loligo* occurs in the spring and summer near shore off southern New England and Long Island. *Loligo* migrates inshore to spawn as the water warms up. Nantucket Sound is the site of intensive trawling for squid by vessels which make short trips, ice the catch, and then deliver it to shore-based processing plants. There is also a significant trap fishery which provides the highest quality squid, since the squid is brailed into the boats alive, not crushed in trawls, and is delivered for processing within hours of being taken from the water.

During 1981 and 1982 Japanese, Italian and American flag processing vessels received squid from small U.S. vessels off Long Island under joint venture arrangements. In 1982 a small U.S. based directed trawl fishing for *Illex* was initiated east of Delaware Bay during July and August.

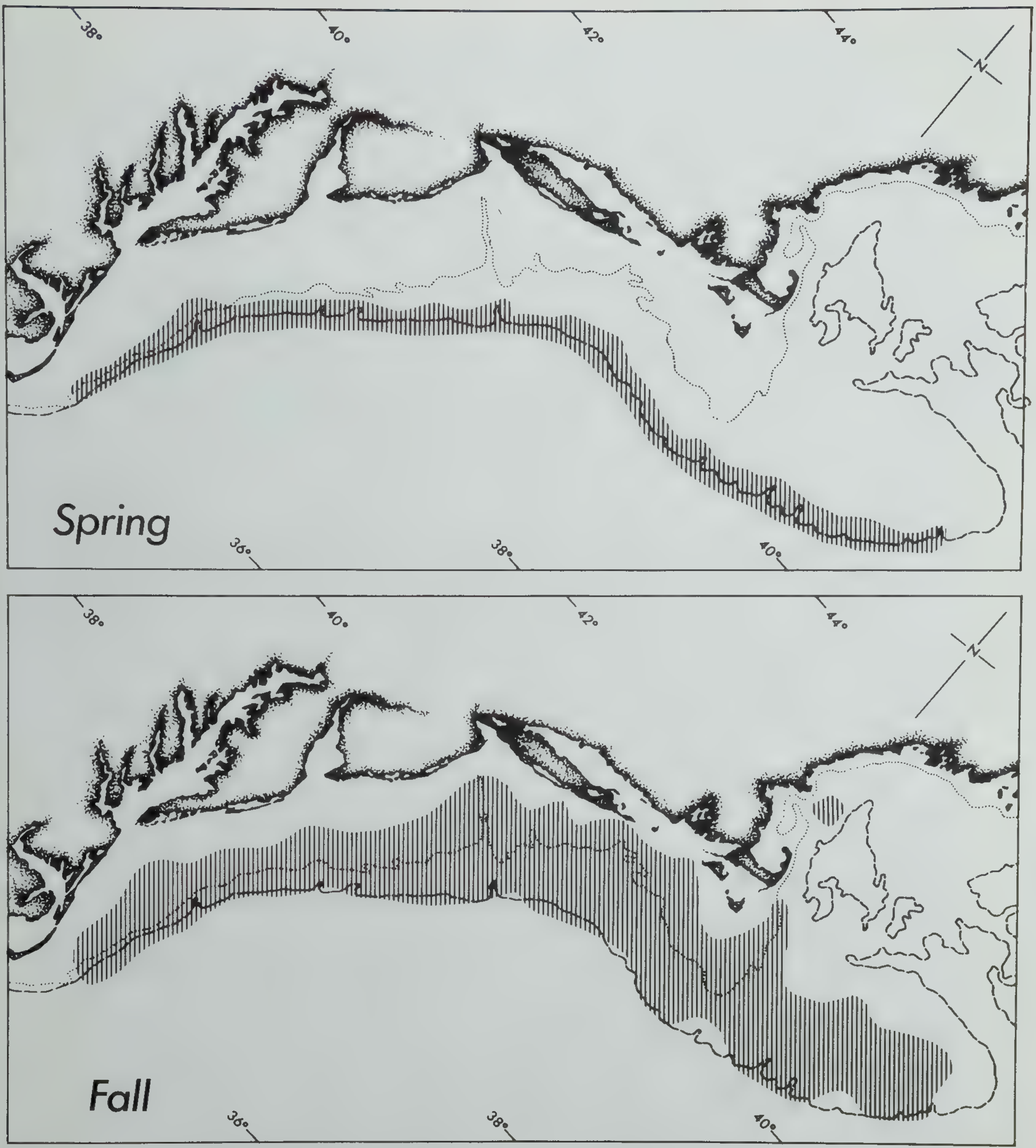

Figure 2. Shaded area represents typical distribution of long-finned squid *Loligo pealei* over continental shelf in the spring (March-May) and fall (September-November) periods. Data have resulted from Northeast Fisheries Center groundfish surveys which do not cover depths of less than 27 metres.

(From Rathjen, 1973)

TABLE 1

Recent Trends in foreign squid catches in U.S. waters (1976-1981)
(in metric tons)

Year	U.S. Harvest (Loligo and Illex)	Foreign Loligo	Foreign Illex	Foreign Total	Grand Total	U.S. Catch As % of Total
1976	3830	20 636	22 564	43 200	47 030	8%
1977	1879	15 586	23 769	39 355	41 234	5%
1978	1700	17 310	9 356	26 666	28 366	6%
1979	5992	13 183	16 426	29 609	35 601	17%
1980	3998	17 944	14 870	32 814	36 812	11%
1981	3618	19 290	14 789	34 079	37 095	10%

Unpublished NMFS data on species composition of squid catches for NW Atlantic.

Potential off the Southeastern United States

The southeastern portion of the United States can be described as that area south of Cape Hatteras extending to the border of Mexico. At this time there is no significant fishery for squids in this area.

Whitaker (1980) described the results of exploratory fishing from a portion of this area and concluded that the development of large scale squid fisheries there is 'highly improbable'. Hixon *et al.* (1980) were not optimistic concerning squid fishery development in the northwestern Gulf of Mexico but listed several species that might be considered. Rathjen (1981) suggested that *I. illecebrosus* may be present in large concentrations in deep water (300-900 m) off Florida and Georgia at certain seasons of the year.

The Orangeback Squid, *Ommastrephes pteropus*, frequently is suggested as an objective for fisheries development as it is broadly distributed over the sub-tropical and temperate Atlantic Ocean (Figure 3).

Western North America

The traditional fishery for *L. opalescens* off the coast of California is conducted seasonally inshore from two locations. During the winter months, November through March, the fishery is conducted at San Pedro (southern area) with light attraction and lift nets; purse seines are sometimes used. Monterey is the traditional center of the northern fishery with most of the landings there being taken by lampara seine (Figure 4) from April to July. The overall landings in the California fishery range from 6 000 to 20 000 tons annually. Most of the catch is usually taken from the Monterey area, but in some years southern California (San Pedro) landings are greater (Kato & Hardwick, 1976).

The California catch is processed either by canning or freezing. Much of the product is exported to various world markets but increasing amounts are utilized by domestic markets. It has been suggested that some expansion of the fishery is feasible, but primary drawbacks include limited existing markets and unpredictable access to the resource (Dewees & Price, 1982).

Bernard (1980), indicated the possible extension of the *L. opalescens* fishery into coastal areas of Washington state and British Columbia. Local aggregations of this species are known from both areas and, if market incentives are identified, fisheries could be developed. Robbins (1982), indicated that a fisherman utilizing light attraction and a 'brail' lift net harvested 45 000 pounds (20 454 kg) in three hours of fishing, off Oregon.

The squid *Berryteuthis magister* also has been identified by Bernard (1980) as a species with some potential off Washington, British Columbia and other areas of the northeast Pacific.

A discussion of the potential development of offshore resources for flying squid *Ommastrephes bartrami* in the northeast Pacific is available in Bernard (1981).

Recent interest has developed in the Gulf of California (Mexico) concerning the exploitation and commercial use of the jumbo squid *Dosidicus gigas*. This species is attracted to light and

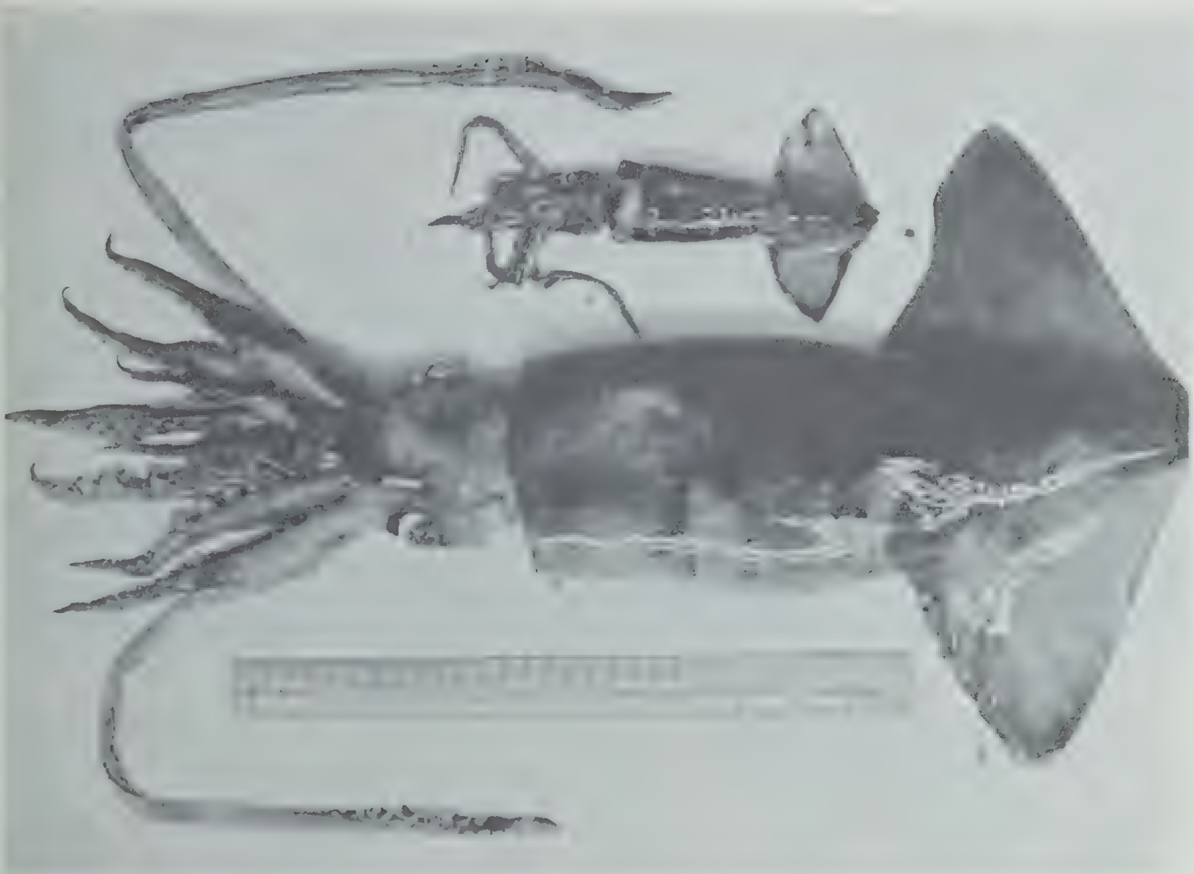

Figure 3. Large and small specimens of the Orangeback Squid (*Ommastrephes pteropus*). This species is widely distributed over the warm oceanic Atlantic.

(Photo: W. F. Rathjen)

was being exploited at the rate of over 22 000 tons during 1980 (Ehrhardt *et al.*, in press). Klett (1982) describes the fishery and plots its growth from incidental levels prior to 1976. The present fishery is seasonal with most production coming from light attraction and jig fishing during the warm months (April-October). Concurrent with fishery development have been sophisticated marketing programs (Blake, 1982).

The major external constraint to expansion of the West Coast squid industry are uncertain markets. Demand for squid has been growing, partly as a result of declining catches from traditional world fishing areas, but supplies over the past few years have increased and become unstable due to new fisheries for a variety of squids in many parts of the world.

North America shows several contrasting situations in terms of developing squid fisheries. These range from comparatively well developed fisheries in the adjacent northwest Atlantic to poorly understood fisheries in the northeast Pacific. The various requirements for fully understanding and managing these resources rarely stand by themselves in terms of assignment of priority, e.g., harvesting technology, processing, assessment, oceanography, biology, conservation and management, marketing and economics. Experience in developing squid fisheries in the northwest Atlantic has demonstrated that progress in any one discipline is to some extent interdependent upon more than one additional area of interest.

Figure 4. Typical small Lampara seine vessel involved in the Market Squid (*Loligo opalescens*) fishery in Monterey Bay, California.
(Photo: J. B. Phillips)

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SUMMARY OF FISHING GEAR AND METHODS EMPLOYED IN THE SQUID FISHERY OF JAPAN

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Abstract

The gear and methods that have been developed in Japan for catching squid, especially *T. pacificus*, are reviewed, with particular emphasis on lamps and illumination.

I. Fishing Gear

(1) *The Jigger* The common type of jigger used in Japan consists of numerous stainless steel hooks attached to the base of a plastic stem (Figure 1). About 30 jiggers are attached to an angling line at intervals of approximately 1 meter. Four lengths of stems, measuring 36, 42, 48 and 54 mm, are used. The 48 mm stem is employed mainly throughout the fishing season. There are certain fishermen, however, who change the size of their jiggers to match the seasonal changes in size and habit of the squids. The length of the hooks used ranges from 0.8-1.2 mm for the common squid (*Todarodes pacificus*) and from 1.2-1.4 mm for the red squid (*Ommastrephes bartrami*). These slightly elongated hooks are utilized in order to prevent excessive escapement. Generally red and green stemmed jiggers are used. In recent years, hollow vinyl stemmed jiggers have been used in conjunction with the common variety. In order to improve the jigging efficiency, one or two small battery-powered lights or 'cyalume lightsticks' are attached to the jigging line.

(2) *The Jigging Line* The jigging line consists of a main line attached to numerous jiggers connected to each other by leaders. The main line is of nylon monofilament or wire 1.35-1.67 mm in diameter, and the leaders are of nylon monofilament 0.74-0.90 mm in diameter. The leaders nearest the main line are slightly thicker than those towards the far end of the jigging line near the sinker.

(3) *The Sinker* The spindle-shaped, iron sinker is attached to the end of the jigging line. The 10-ton class of squid fishing vessels use a 750 g sinker, while the 99-ton class vessels use a 1 kg sinker.

II. Fishing equipment

(1) *The Automatic Squid Jigging Machine* The automatic jigging machine (Figure 2) has been widely used since about 1964. At present, most squid fishing vessels are equipped with these jigging machines. The machine is either electrically driven by the main engine (generator) or by a hydraulic system, and each machine controls one or two jigging lines. The vertical jigging motion of the jigging lines is achieved by the cam-shaped rotating drum; the speed of this motion is adjustable. When entanglement between neighbouring jigging lines occurs, the rotating drum can be stopped immediately or free-wheeled. Moreover, the lines can be adjusted to match fishing depths and the degree of jigging motion can be controlled. In recent years, vessels have been developed with a completely remote controlled system operated from the bridge.

(2) *Fishing lamps* Incandescent lamps (200 v, 3-4 kW) are used as the primary attracting light source in the squid fishery. The 99-ton class vessels, which are the mainstay of the squid fishing fleet, usually are equipped with 50 of these lamps (Figure 3) for a total illuminating power of 150 kW. In recent years, however, the smaller and more economical Halogen lamp has gained widespread popularity.

(3) *The Sea Anchor* Squid jigging is conducted with the boat stopped, so it is necessary to use a sea anchor (parachute anchor) (Figure 4) and spanker sail to maintain the vessels position against the wind and current. Spankers are most effective in smaller vessels, though the 99-ton class vessels also are equipped with them.

Memoirs of the National Museum Victoria, No. 44, 1983.

Figure 1. Common type of squid jigger.

Figure 2. Automatic squid jigging machines.

Figure 3. Fishing lamps (incandescent lamps: 200V, 3Kw).

Figure 4. Sea-anchor (parachute anchor).

III. Fishing Method

Fishing grounds are determined according to information obtained from the Information Service Center, and location is based on the fishing and oceanographic conditions of the previous few days. Water temperature recordings conducted aboard each vessel, effective use of the fish finder (echo sounder), and radio communications between vessels all are taken into consideration when determining fishing grounds.

Before actual fishing commences, the fishing lamps are lit and the vessel's position established through deployment of the sea anchor and spanker. The length of the jigging line is adjusted so as to match the depth of the squid aggregation. Due to the utilization of the automatic squid jigging machine, the role of the crew is dedicated to processing the catch.

Smaller vessels that undertake short cruises store the squid in ice. The large vessels, with cruising capacities of between 20-30 days, are equipped with freezing facilities.

IV. Fishing Lamps and Light Attraction for Squid Jigging

(1) *The Utilization of Fishing Lamps in Squid Jigging* Fishing lamps used aboard squid fishing vessels are mainly incandescent, consisting of 200 V-3 kW bulbs. In recent years, the use of mercury lamps has become widespread but this has not led to an improvement in the catching efficiency. Besides, the high cost of these lamps has contributed to a decline in their use. It was only after this that highly economical halogen lamps were developed, consisting of bulbs one-thirtieth the size of the incandescent bulbs. At present, the use of halogen lamps abroad large squid fishing vessels is steadily increasing. Aboard medium and small sized fishing vessels, too, halogen lamps now are used in conjunction with incandescent lamps. The use of metal-halide lamps has been considered recently, and experiments in their practical use are now being conducted.

(2) *The Underwater Distribution of Light for All Types of Fishing Lamps* The underwater intensity of an incandescent lamp used by a small squid fishing vessel is first measured and its equal-illumination curve is then drawn (Figure 5). The underwater illumination distribution is found to have a steep gradient for dark areas, but is approximately 1 lux directly under the hull of the ship. Directly under the jiggers, for depths greater than 10 m, light intensity is found to decrease within a range of less than 1 lux (Ogura *et al.*, 1973). Horizontal light distribution is found to form a 'butterfly' shape. The underwater light distributions of incandescent, halogen and mercury lamps of an illuminating power of 3 kW each, are found to have, in the cases of the incandescent and halogen lamps for 10, 5 and 1 lux respectively, with highly similar equal-illumination curves; but in the case of the mercury lamps the light distribution is found to be very widespread—for values less than 20 lux, the light distribution approximately doubles (Figure 6 a-c).

(3) *The Effects of Arrangement and Height in Fishing Lamps* Squid generally are observed to gather within shaded areas formed by the shadow of the vessel. The fishing jiggers pass over rollers positioned on the gunwales and through the common boundary area of the dark and lighted areas. Consequently, the relationship between the position of the rollers and the arrangement and the height of the lamps above the deck is important (Ogura, 1973).

A number of experiments have been conducted in order to determine the relationship between the catch and light penetration of fishing lamps. Results show that jiggers suspended in bright areas experience extremely low catches, whereas jiggers suspended through the border between dark and lighted areas yield particularly good catches (Kawamura, 1970). Squid fishing vessels are numerous with either a single or double row of lamps running from stem to stern. Research on changes in the arrangement of the lamps and the corresponding effects on catches shows that a double row of lamps produces better catches than a single row (Karube & Takahashi, 1977).

(4) *The Effects of the Illuminating Power of Fishing Lamps on Catches* The relationship between the illuminating power of fishing lamps

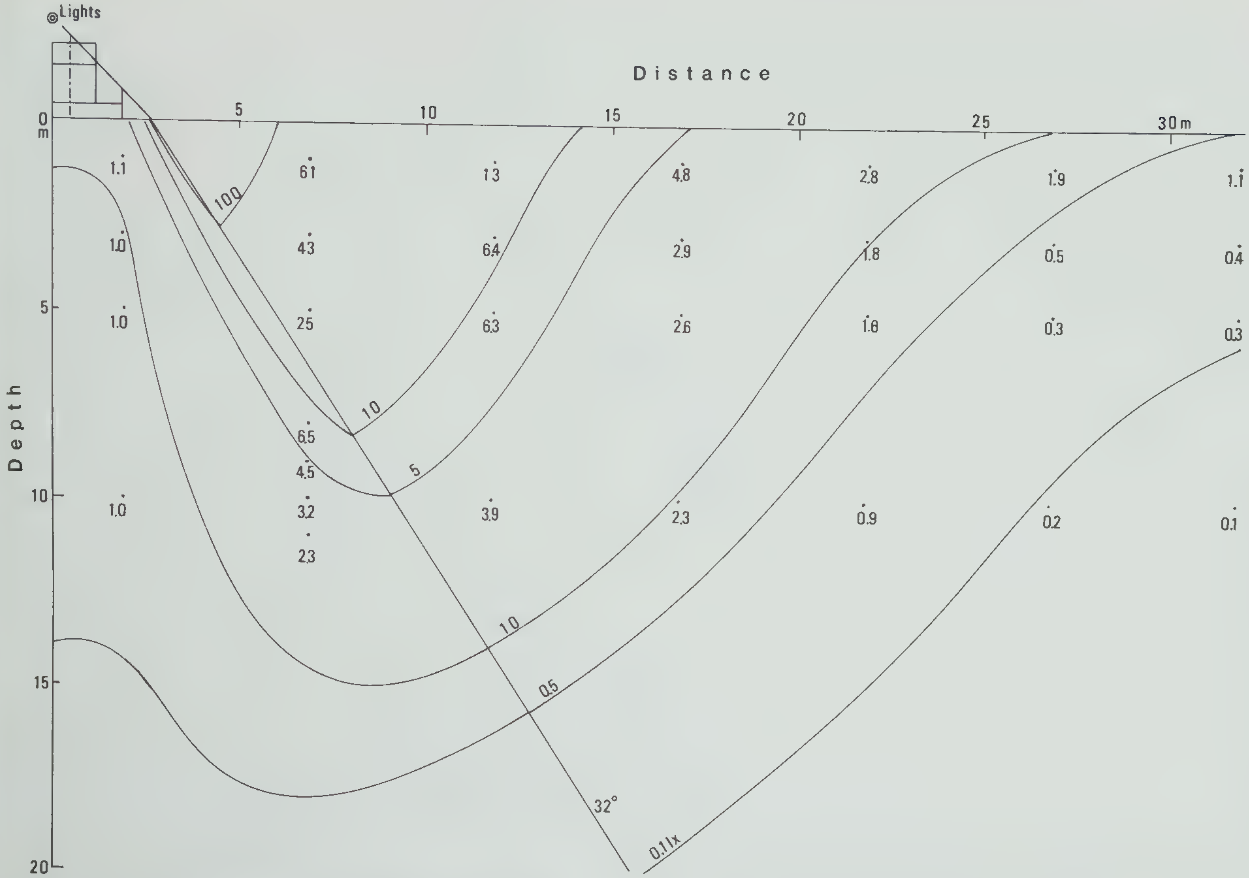
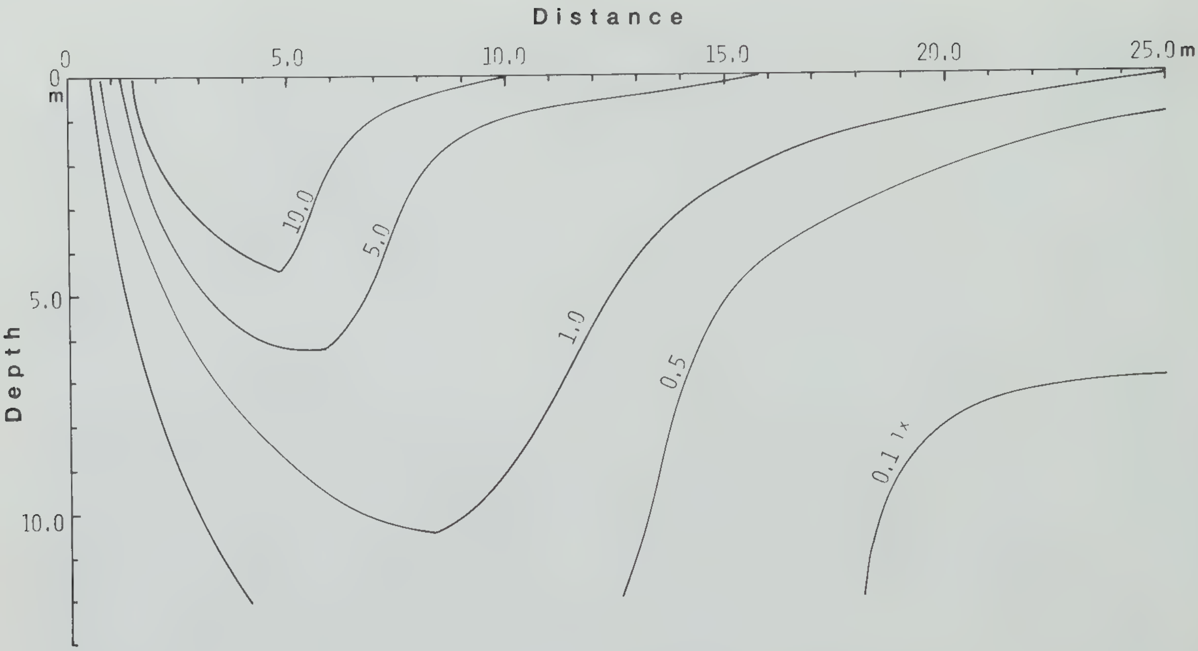


Figure 5. Vertical distribution of underwater illumination with 9 bulbs of 1-2 Kw incandescent lamp in one row along the centre of the boat (5 ton).

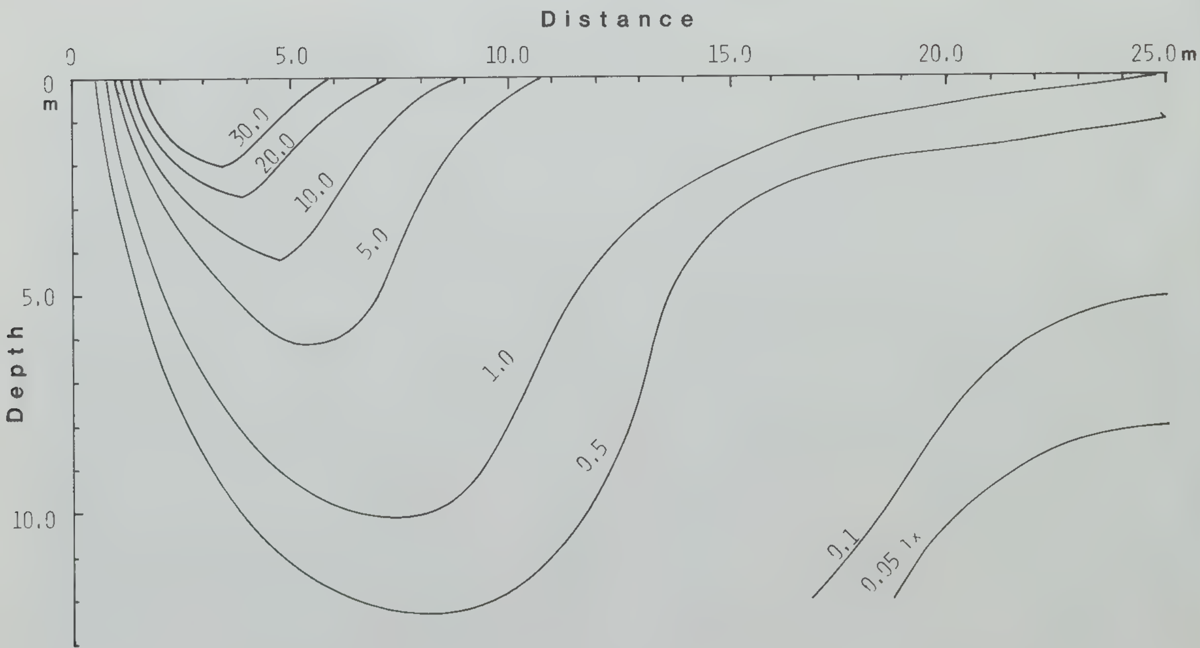
and the squid catches has been widely investigated (Karube *et al.*, 1974). Within the 10-20 ton class of fishing vessels, the average illuminating power of a single bulb has steadily increased from 1.6 kW in 1972 to 2.3 kW in 1977. In the relationship between illuminating power and catch efficiency, a high efficiency index of approximately 50 kW is optimum (Karube, 1979). Among the 60 ton class of medium sized vessels, the average illuminating power also has quadrupled over the last six years to 160 kW. In the illuminating power—catch efficiency relationship, an illuminating power of greater than 100 kW produces no increase in the efficiency index (Figure 7) (Ogura *et al.* 1979). Accordingly, there are clear limits to the illuminating power-catch relationship.

(5) *The Effects of Underwater Lamps on Catches* A number of experiments using underwater lamps in the squid fishery also have been conducted (Miura, 1951; Ogino, 1968), using green, red and pink neon tubes. The green tubes result in good catches; a drop in the squid catch during constant illumination is overcome by switching the underwater lamps on and off (Karube & Miyajima, 1978 a, b). This method, however, has not been put into practical use as yet.

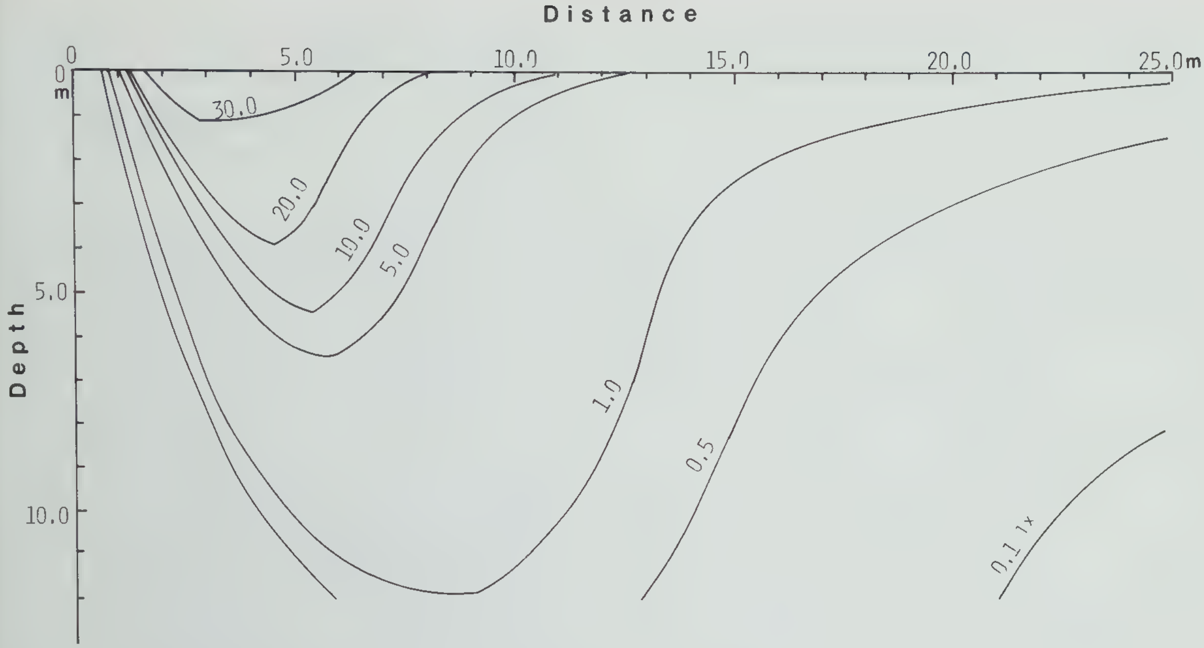
(6) *The Behaviour of the T. pacificus to Light* The reactions of the common squid to light have been investigated over a long period of time. Even so, data and knowledge acquired have been limited. The following experiments concerning the reactions of the common squid to light have been conducted by the author. In the case of incandescent lamps with differing illuminating powers of 500 w and 100 w, squid



Incandescent Lamp 6-a



Halogen Lamp 6-b



Mercury Lamp 6-c

Figure 6-c. Underwater light distribution with mercury lamp.

were seen to gather around the 100 w lamps, whereas they tended to scatter away from the 500 w lamp. For differing voltages of 100 v and 130 v, the squid prefer the higher voltage. In the case of the mercury lamps, during the time taken to achieve maximum luminosity the squid frequently are observed to dart to the darkest area, which is located at the opposite side of the light source. In the case of green fluorescent lamps, the squid concentrate directly below the light sources; but in comparison with the incandescent lamps the squid seem to disperse slightly (Table 1) (Nasumi *et al.*, 1973; Ogura & Nasumi, 1975).

Figure 6-a. Underwater light distribution with incandescent lamp.

Figure 6-b. Underwater light distribution with halogen lamp.

TABLE 1

Behaviour of *T. pacificus* in response to different light sources

Light source	Distance from light source	Size of squid school
Incandescent		
100V 100W	2.33^{m}	2.51$^{m^2}$
130V 100W	3.48	3.32
100V 500W	2.99	3.98
Halogen		
Transp. 40W	1.98	3.39
White 40W	2.65	4.31
Fluorescent		
20W	2.10	2.20

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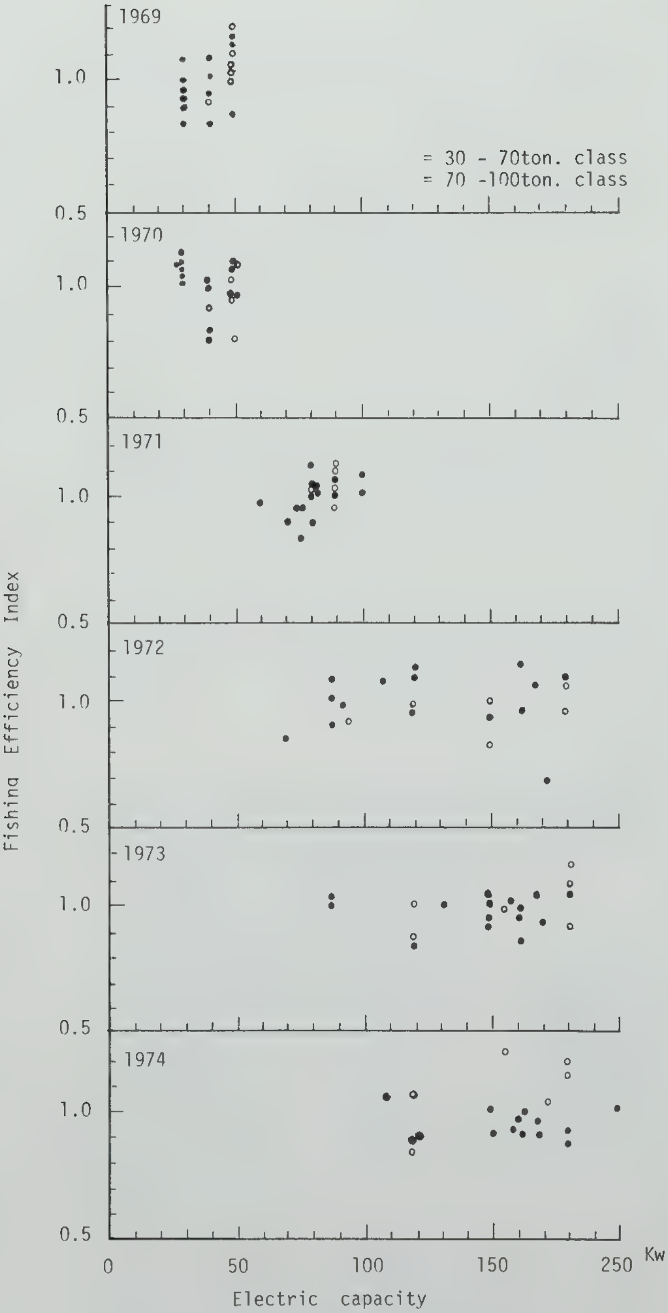

Figure 7. The relationship between the electric capacity of generator and the fishing efficiency index.

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FISHERY, BIOLOGY AND STOCK ASSESSMENT OF *OMMASTREPHES BARTRAMI* IN THE NORTH PACIFIC OCEAN

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Abstract

Fishing for the squid, *Ommastrephes bartrami* in the Pacific waters adjacent to Japan began in 1974. By 1978 the *O. bartrami* catch had increased to about 150 000 tons, making it second in squid catch in Japan, surpassed only by *Todarodes pacificus*. Since the establishment of the ordinance for fishery control by the Japanese Government in 1979, the fishery has been by jigging in the waters west of 170°E and by drift gilnetting in the waters east of 170°E in the Pacific north of 20°N.

In the north Pacific, *O. bartrami* is distributed extensively between Japan and North America, and the squid populations in these waters consist of several groups in different stages of growth. Population densities in the north Pacific are high in the waters west of 165°E and east of 170°E, and low in the area between 165°E and 170°E. It is therefore assumed that the two populations are independent of each other.

Based on ecological studies of the *O. bartrami* population in the waters west of 165°E, the squid migration follows the movement of the Kuroshio branch current, northward in spring-summer and southward in fall-winter. The squid fishing season is mainly from summer to fall; the fishing grounds are in the warm branch of the Kuroshio current and in the boundary zone of the warm branch and the cold Oyashio current. In the fishing grounds, a spring layer with temperatures over 10°C forms in the upper stratum, and squid generally congregate in and above this layer. *O. bartrami* feeds mainly on fish, most commonly on Lantern fish, Myctophidae. The growth of *O. bartrami* is remarkably rapid; squid hatched in the Kuroshio counter-current area grow to juveniles during the northward migratory season from spring to summer and to adolescents in the waters off eastern Hokkaido from summer to fall. In the southward migratory season, both sexes become adult, and when the gonads begin to mature, the mantle lengths have increased to 29-35 cm. The life span of *O. bartrami* is estimated to be about one year, as the male dies after copulation and the female after spawning.

Judging from statistical analysis and differences in mantle length of the squid caught every year, it is estimated that the resource of *O. bartrami* in the waters west of 170°E is declining. This is considered to be caused by over fishing.

Introduction

Until 1974, *Todarodes pacificus* Steenstrup was the major squid caught in waters adjacent to Japan, followed by sepiids and loliginids. In 1970, the catch of *T. pacificus* started to decline and *Ommastrephes bartrami*, which had been neglected until then, became a new target species to cover the decrease of *T. pacificus*. Beginning in 1974 the annual catch of *O. bartrami* continued to increase until it now occupies second position in the squid fishery following *T. pacificus*. After several years of fishing for this species, however, a remarkable change appeared in the condition of the population, and a method is urgently needed to estimate and assess the resource of *O. bartrami* for proper control.

The condition of the *O. bartrami* fishery is discussed in this paper. Information on the biology and changes in the resource also are presented.

1. General description of Fishery

(1) *Catch.* The presence of *O. bartrami* in the Pacific Ocean adjacent to Japan has been well-known for a long time. However, a high abundance was demonstrated for the first time in 1973 when cooperative investigations were initiated by the Fisheries Research Laboratory and the Fisheries Experimental Station. Based on this investigation the fishery for *O. bartrami* began in 1974. The *Ommastrephes* fishery developed raidly with improved food processing techniques and increased demand. The catch was 17 000 tons in 1974, increased each year and reached 151 000 tons in 1978 (Fig. 1). This enormous increase in catch was achieved mainly by expanding the fishing grounds, increasing the number of fishing boats, and improving fishing gear and methods. Drift gillnet fishing began in 1978 and was a great success. Nevertheless, in 1979, the catch decreased for the first time to 124 000 tons. Of these catches, 40 000-50 000 tons are estimated to be by the drift gillnet fishery for the years 1978 and 1979.

(2) *Fishing season and fishing grounds.* The jigging fishery for *O. bartrami* usually begins in July, peaks from August to October, and

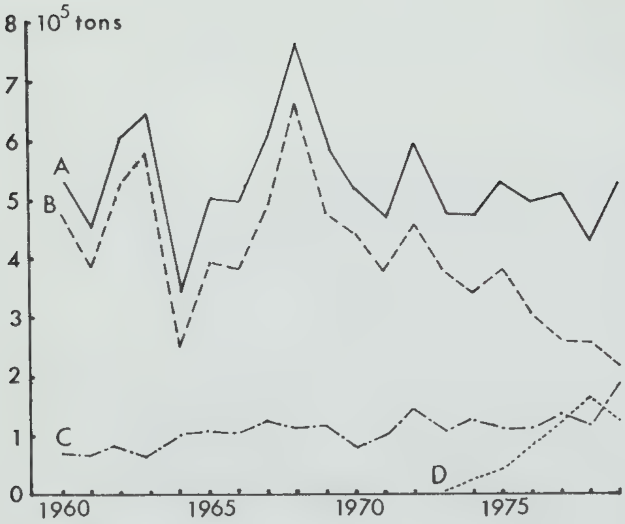


Figure 1. Squid landings in Japan
A: Total catch B: *Todarodes pacificus*
C: Other species (Sepiidae and Loliginidae)
D: *Ommastrephes bartrami*

rapidly declines in November. The squid jigging ground has continued to expand eastward from year to year. The eastern limit of the jigging ground which was 150°E in 1974 and 1975, extended to about 165°E in 1978 and 1979 (Fig. 2).

Let me illustrate seasonal changes of the jigging grounds in 1978. During the early season (July) the main ground was situated between 39° and 40°N Lat. and between 152° to 160°E Long. in the North Pacific. A small ground appeared also along the Joban Coast. During the height of the fishing season, the jigging grounds shifted northward to 40° to 46°N Lat., making three major grounds: west of 149°E, 150°-159°E and 160°-165°E. Small-sized boats of less than 30 tons operated west of 149°E, medium-sized boats between 30 and 99 tons fished west of 159°E and large boats over 100 tons fished between 150° and 165°E. From late October through November, the grounds east of 159°E diminished and moved southward or westward. The grounds west of 150°E also moved southward in November and December (Figure 3).

The drift gillnet fishery of *O. bartrami* began in September of 1978 and a number of boats took part in this fishery in the area west of 150°E until December of that year. However, the fishery was totally prohibited in the area north of 20°N and west of 170°E from January of 1979. Thus, the main ground from August to December of 1979 changed its location to the area 40°-47°N and 170°E-173°W.

(3) *Fishing gear and methods.* Jigging gear and fishing methods for *O. bartrami* are similar to those for *T. pacificus.* Both are principally fished at night using bright lamps and automatic jigging machines supplemented by hand line jigging. However, the jig hooks are larger than those for *T. pacificus* in order to prevent *O. bartrami* from dropping off while being raised. A large boat or a boat with large crew generally is superior in fishing efficiency, because the efficiency depends on the number of jigging machines and hand line jiggers. The fishing efficiency of drift gillnet fishing is 2-4 times higher than jigging. In the latter method, the efficiency per boat is controlled by the dimensions and mesh size of the net.

2. **Biology**

(1) *Distribution. Ommastrephes bartrami* is the most widely distributed of all the Ommastrephidae. It is recognized in the Pacific, Indian, and Atlantic Oceans. It occurs only rarely off east China, in the Japan, Okhotsk, and Bering Seas, in contrast to its extensive distribution in the North Pacific Ocean between Japan and North America (Figure 4).

In the waters adjacent to Japan the population of *O. bartrami* is most dense in the northern branch of the Kuroshio Current and its frontal zone (36°-38°N Lat. and 144°-156°E Long.) between May to June. In July through December the main distribution area is assumed to be in the area between 39° to 46°N and west from 165°E, first northward and northeastward from July to September, then diminished southward and southwestward from October to December. Population density is highest in the boundary zone between warm and cold waters where isothermal lines converge. This trend is limited to areas where the surface water temperature ranges from 15°-°24°C (July to August) and 10°-22°C (September to December). Distribution from January through May has not been elucidated yet. However,

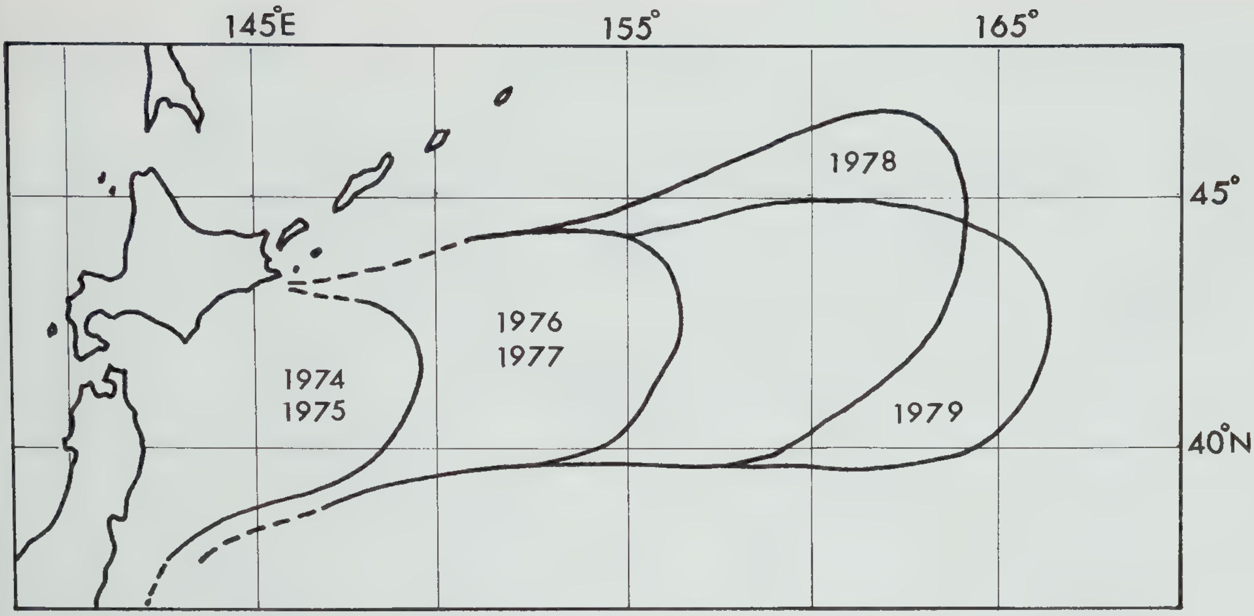


Figure 2. *Ommastrephes bartrami:* General view of the expansion of the squid jigging ground.

fairly dense schools of mature squids are sometimes found along the coast of the Joban district where surface water temperatures are 15°-18°C, and less often in the sea area 25°-34°N and 136°-152°E from January to February. During summer and fall the squid migrate to the surface waters to feed, whereas, in winter and spring they move to deeper water to breed. This is thought to be the reason that distribution density is high in summer and fall and low in winter and spring.

During the feeding season, the vertical distribution of *O. bartrami* probably is related to the depth of the 10°C isotherm. The line lies as deep as 150 m though usually it is less than 70 m in warm Kuroshio water. The depth is roughly equal to the lowest depth of squid catch. In the cold water area of Oyashio, it is believed that most of the squid are distributed in and above a layer 30-50 m deep where the spring layer over 10°C is formed.

In view of the high yield obtained by drift gillnets, the squid population during the night appears to be situated at a depth of approximately 10 m. Distribution during the day has not been confirmed, but based on knowledge on other Ommastrephidae, it is thought to be into deeper water. Hence, they probably undergo a daily vertical migration.

(2) *Population structure*. Squid were collected during August and September by test jigging in the North Pacific Ocean between Japan and North America and mantle lengths of samples caught every 10 degrees of longitude were compared. According to these studies, the squid are distributed in three groups: (A) in the area west of 160°E; (B) in 180°-140°W; (C) in 140°-130°W. The mantle lengths in group A are large, ranging from 15-39 cm, mostly between 20 and 28 cm. The lengths of group B are 19-33 cm, mostly 21-25 cm. In group C, the range is 23-47 cm, the majority being 35-42 cm (Figure 6). Other samples were collected by drift gillnet (a set of ten mesh sizes between 48 and 157 mm) in the area 180°-174°W during July, and their lengths were distributed over a wide range between 19 and 52 cm. In these samples, larger squids generally were caught in the north and smaller ones in the south (Figure 7). Such a broad distribution of mantle lengths suggests the existence of several groups in different growth stages in the North Pacific.

Results of the jigging survey for *O. bartrami* during May and June in the waters west of 180°E (Figure 5) indicate the distribution is highest in areas west of 156°E and east of


45°
40°
July
Aug.
Sept.
45°
40°
Oct.
Nov.
Dec.
N
145°E
150°
155°
160°

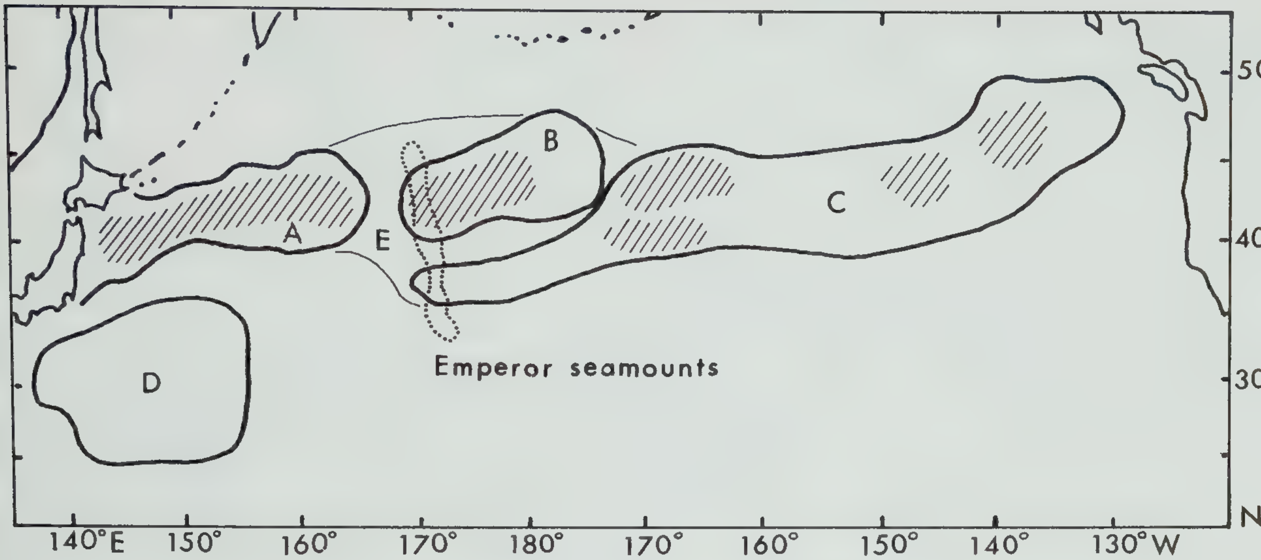


Figure 4. Main distribution areas of *Ommastrephes bartrami* in the North Pacific Ocean.
A: Jigging ground B: Drift gillnet fishing ground
C: Distribution area of squid taken by research vessel
D: Distribution area of mature female squid taken by research vessel
E: Rare distribution area
High density of squid population.

170°E and lowest in between these areas. During the fishing season after July, the density is highest in the jigging area west of 165°E and also in the drift gillnet area east of 170°E and low in between (Figure 4). Moreover, in tagging experiments in the area west of 165°E no tagged squids were recaptured to the east of 170°E (Figure 10). These results and seasonal changes of the fishing ground suggest that the population west of 165°E rarely interacts with the population east of 170°E.

The population in the area west of 165°E consists of two to three size classes (Figure 9). Difference in size classes can be explained in terms of either age differences or independency. However, since this species does not live more than one year and the breeding season lasts from winter through spring, it can be assumed that the difference probably reflects variations in the time of hatching.

Figure 3. *Ommastrephes bartrami*: Monthly jigging ground formation in 1978.

(3) *Movement and migration.* The distribution of *O. bartrami* from summer through winter is concentrated principally in and around the area where the warm water branch derived from the Kuroshio runs northward. This suggests that squid migrations follow the movement of the Kuroshio branch, namely north- and northeastward in summer, and south- and southwestward in fall. This prediction was verified by release and recapture experiments of tagged squids. Squid released during May and June in the area between 36°-38°N and west of 155°E mostly moved northeastward and were recaptured in the area between 40°-45°N and 145°-162°E. Those released in July and August also generally moved northeastward and eastward. On the other hand, the squid tagged and released in the area 42°-44°N and 149°-154°E during September and October moved southward and southwestward (Figure 10). The average distance travelled per day was estimated to be approximately 5 miles from May to August, one mile from August to October, and 10 miles from October to December.

The tagging experiments, seasonal change of distribution, marine environments, and development-growth relationship of squids (discussed later) suggest the following pattern of squid migration in the area west of 165°E. Squid larvae, which are generated during winter

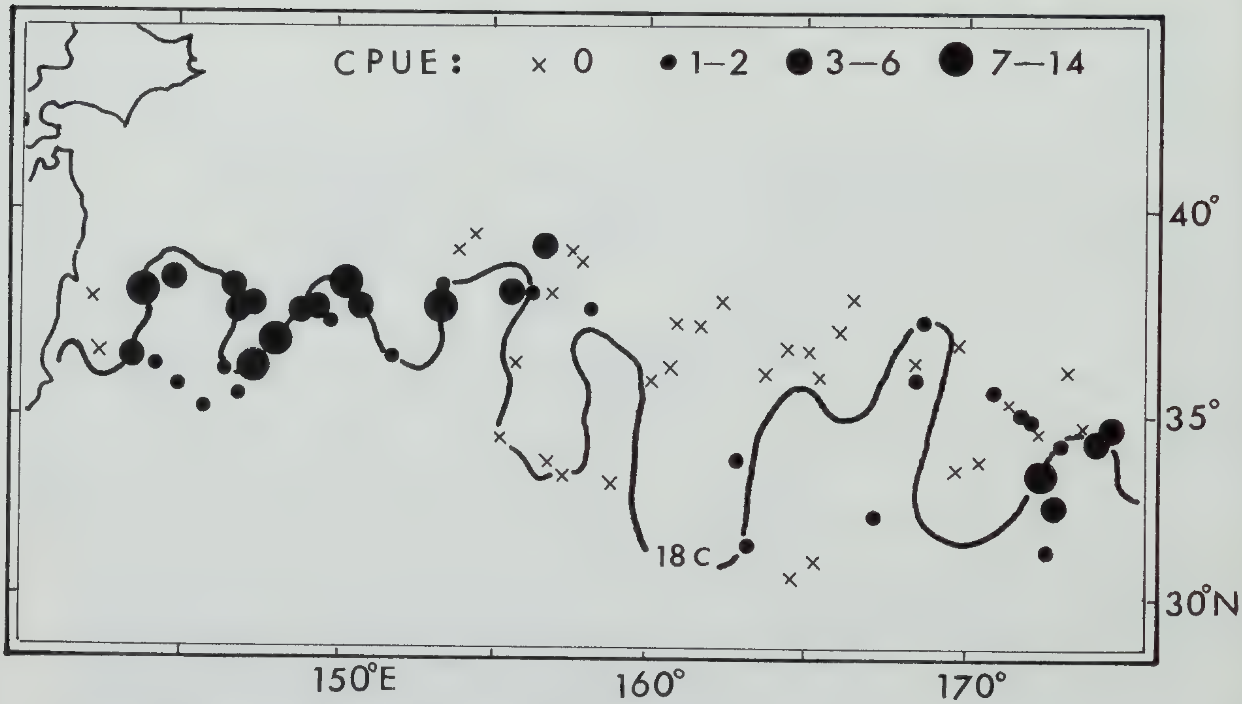
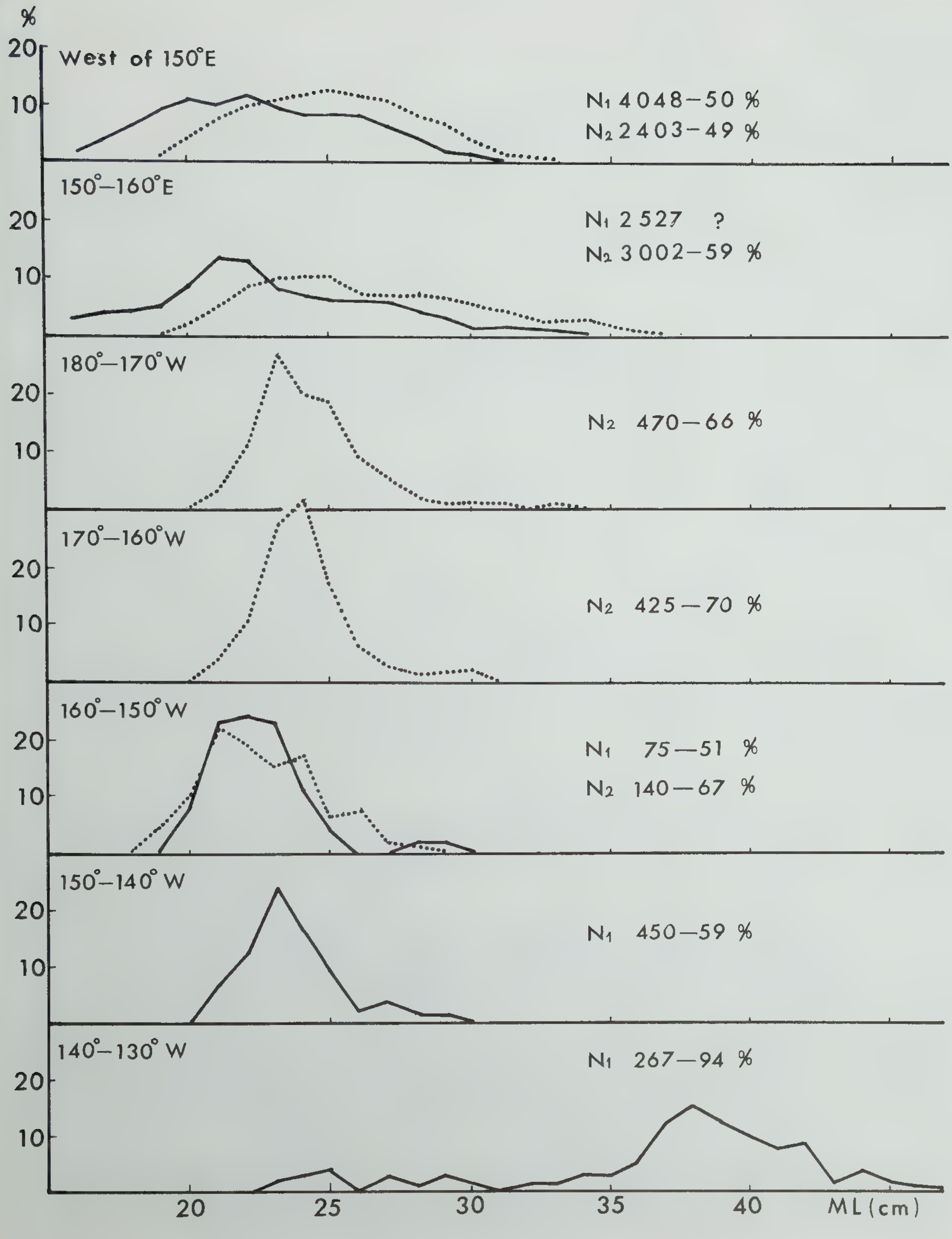


Figure 5. Relationship between distribution of *Ommastrephes bartrami* and the May and June front of the Kuroshio.
CPUE: Number of squid per one jigger an hour.

and spring in the area of the Kuroshio countercurrent south of 35°N and west of 155°E, supposedly remain there or in and near the Kuroshio until they become juveniles. The juveniles probably then move northward to the front of the Kuroshio. The population, which enters the subadult stage from May to August, migrates northward and northeastward through the area 35°-40°N where the Kuroshio meets the Oyashio. The main route of migration proceeds along the north warm water branches derived from the Kuroshio, in the areas 144°-146°E, 148°-151°E, and 154°-156°E. Populations of immature squid are distributed in the surface warm water area in and near the front of the Oyashio in 40°-46°N from August to October. After October and November, most of the squid attain the premature stage and change their migration courses southward and southwestward, while surface warm waters retreat southward due to the progress of cold water from the Oyashio. The relationship between the southerly course of migration and sea conditions is not yet clear. Grown and mature squids start the southerly migration. Since males mature earlier than females, they presumably depart southward earlier than females. During winter and spring they are thought to return to their hatching place, the area of the Kuroshio counter current, for spawning. Although the precise conditions and locations for spawning are still unknown, there are several possible areas such as shoal, reef or insular shelf margin; areas with uneven bottom topography such as seamounts, ridges or basins; and surface layer or midwater of the open sea.

(4) *Growth and life span.* Analysis of monthly mantle-lengths of populations caught in the area west of 165°E indicates that until July the size of females is equal to that of males. The females gradually grow larger than the males after August. The female-male mode of mantle

Figure 6. Mantle-length compositions of *Ommastrephes bartrami* in the North Pacific Ocean.
—— Aug. (N_1), ... Sept. (N_2)
Number of squid measured. Percentage: Females



%
West of 150°E
N1 4048—50 %
N2 2403—49 %
150°—160°E
N1 2527 ?
N2 3002—59 %
180°—170°W
N2 470—66 %
170°—160°W
N2 425—70 %
160°—150°W
N1 75—51 %
N2 140—67 %
150°—140°W
N1 450—59 %
140°—130°W
N1 267—94 %
20
10
20
25
30
35
40
ML (cm)

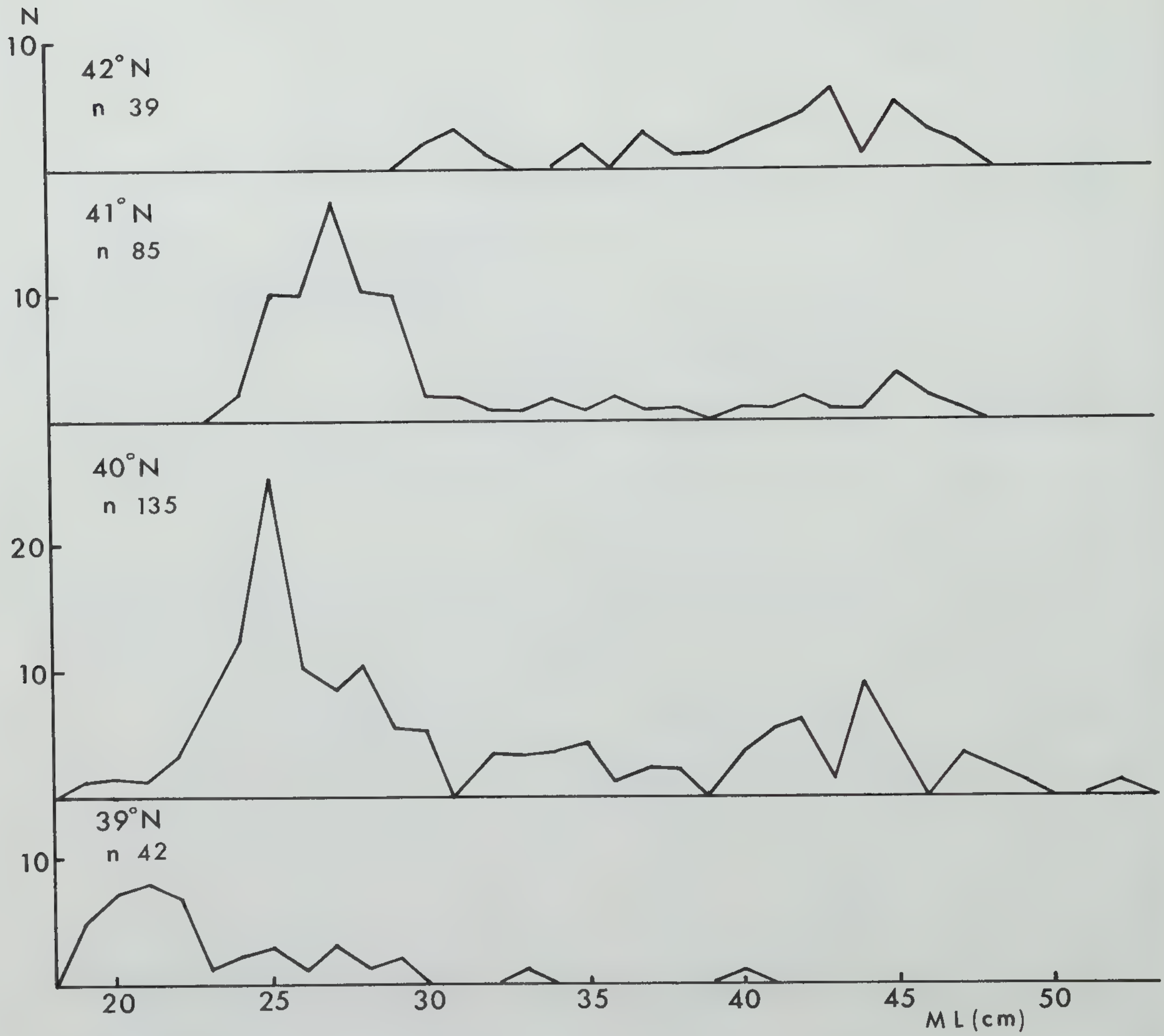
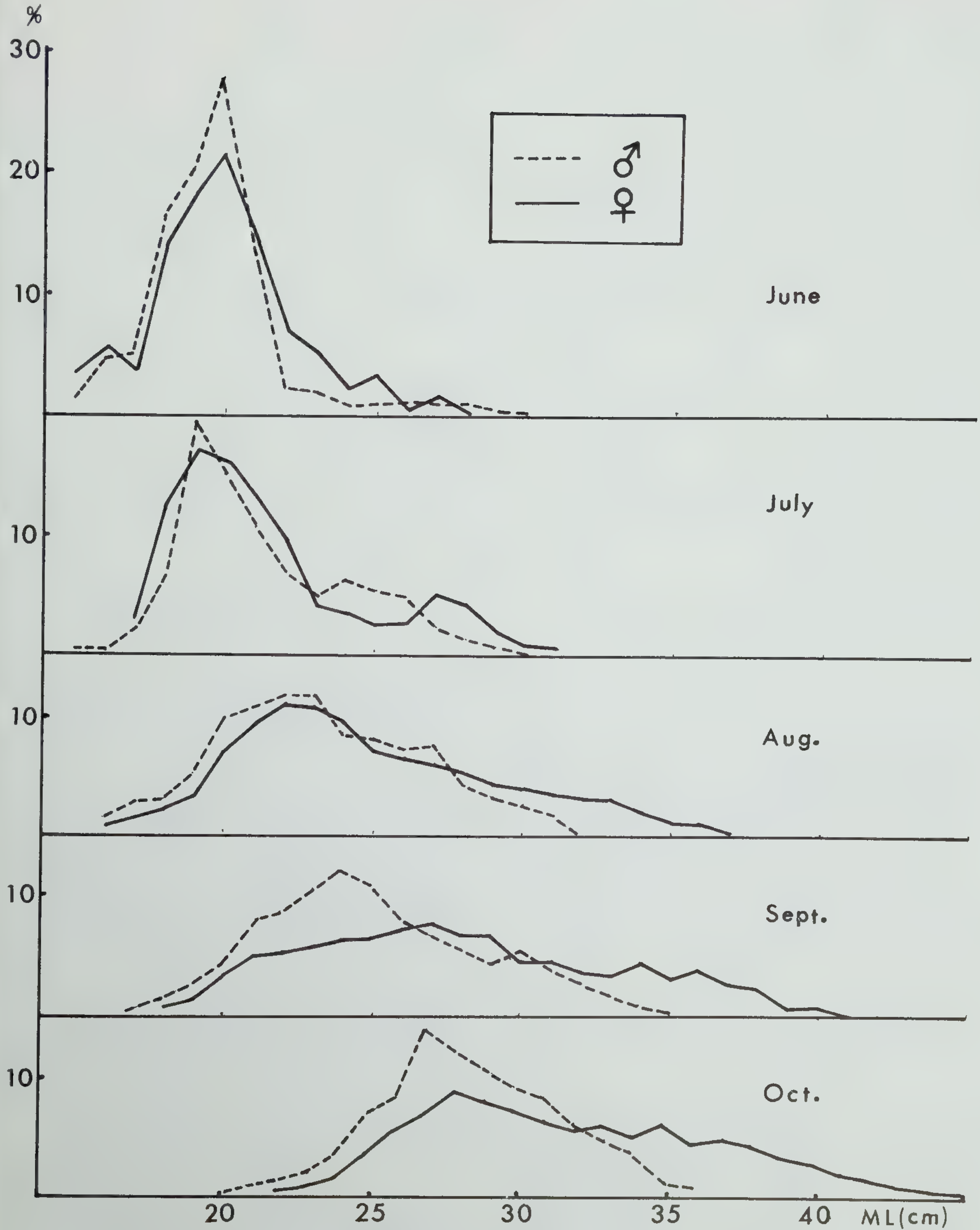


Figure 7. Mantle-length compositions of *Ommastrephes bartrami* in the middle sea area of the North Pacific Ocean. (Samples taken by drift gillnet ten mesh sizes combined, July, 1978.)

length composition increases each month, from 18-22 cm in June to 25-40 cm in October (Figure 8). The monthly increase in mantle length reflects the growth of *O. bartrami*. The monthly growth rate of immature to early adult squid during June and October was 3-4 cm in the fast growing group and 2-3 cm in the slow growing one (Figure 11). Among the tagged squids which were released from May to July and were recaptured from July to October, the rate of growth in mantle length showed a wide range of 1.5 to 8.1 cm per month. Three individuals showed remarkably large rates of 5 to 8 cm (Table 1).

In the months from July to October, most males and females are immature. Males begin to mature so rapidly in November, that their growth rate decreases. Both sexes mature at

Figure 8. Monthly mantle-lengths of *Ommastrephes bartrami* taken by jig west of 165°E in the North Pacific Ocean, 1978.


%
30
20
10
10
10
10
10
June
July
Aug.
Sept.
Oct.
♂
♀
20
25
30
35
40
ML(cm)

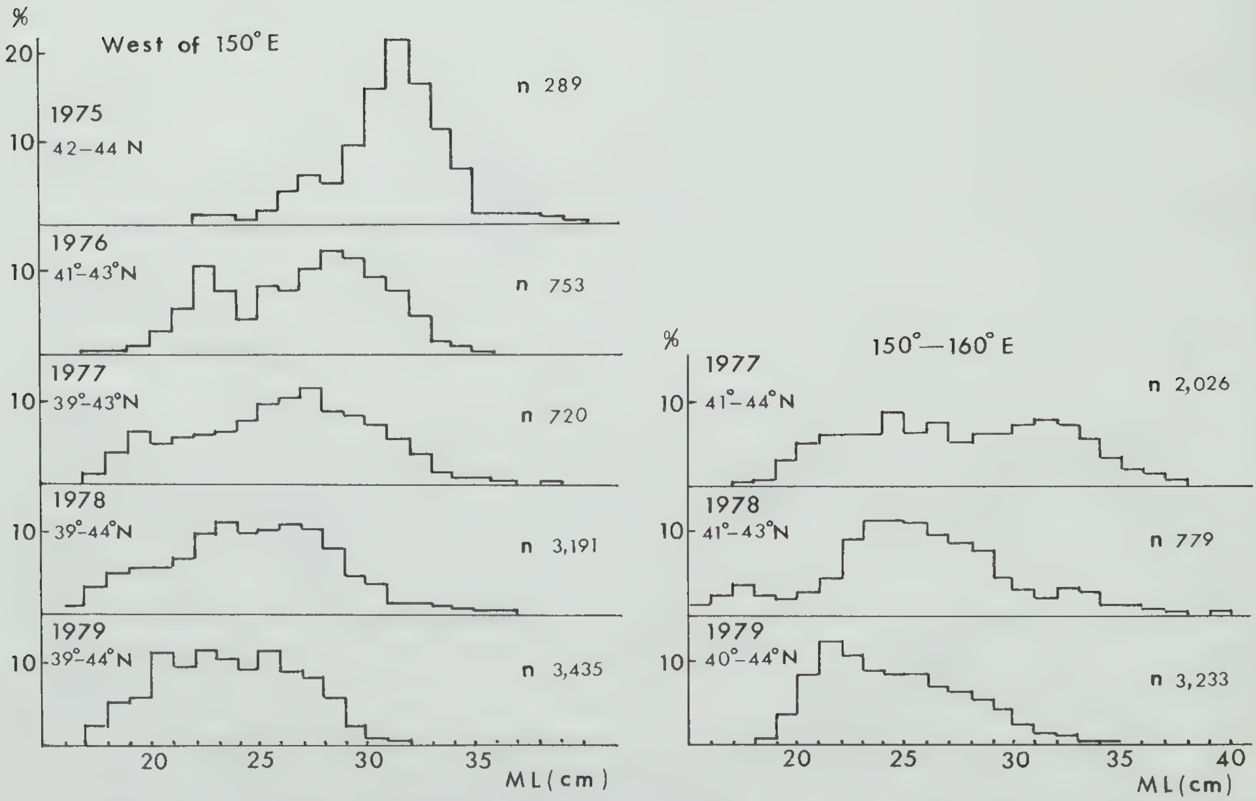


Figure 9. Mantle-length comparisons in late August to early September for the years 1975-1979.

mantle lengths between 29 and 35 cm by January through April. Females reach maturity one to three months later than males. Therefore females keep growing even after November at a rate of 1 to 2 cm per month. The mantle lengths of mature squid collected from January through May measured between 39 and 49 cm.

Based on observations of growth and maturation and on the fact that no tagged squid have ever been recaptured after one year of release, it can be concluded that the males die afer copulation, and females after spawning. Their life span is estimated to be about one year.

(5) *Feeding habits.* The stomachs of *O. bartrami* contained mainly fishes irrespective of the time of capture. Lantern fishes comprised the dominant element followed by sardines, mackerel larvae and sauries. Squids comprised 18-30% of the contents and consisted of:

TABLE 1

Increase in mantle-length of *Ommastrephes bartrami* estimated from tagging experiments.

Release		Recapture		Days to recapture	Increase of mantle length per month
Date	Mantle length	Date	Mantle length		
1977, 5, 24	16-18 cm	1977, 8, 18	23 cm	86	1.7-2.4 cm
1978, 6, 7	16-20	1978, 7, 15	18	38	– 1.6-1.6
1978, 6, 7	16.5-20.5	1978, 8, 8	30	62	4.8-6.8
1978, 6, 9	16-21	1978, 8, 28	38	81	6.3-8.1
1978, 6, 10	19-23	1978, 10, 18	48	131	5.7-6.6
1977, 6, 12	17-24	1978, 9, 2	28	82	1.5-4.0

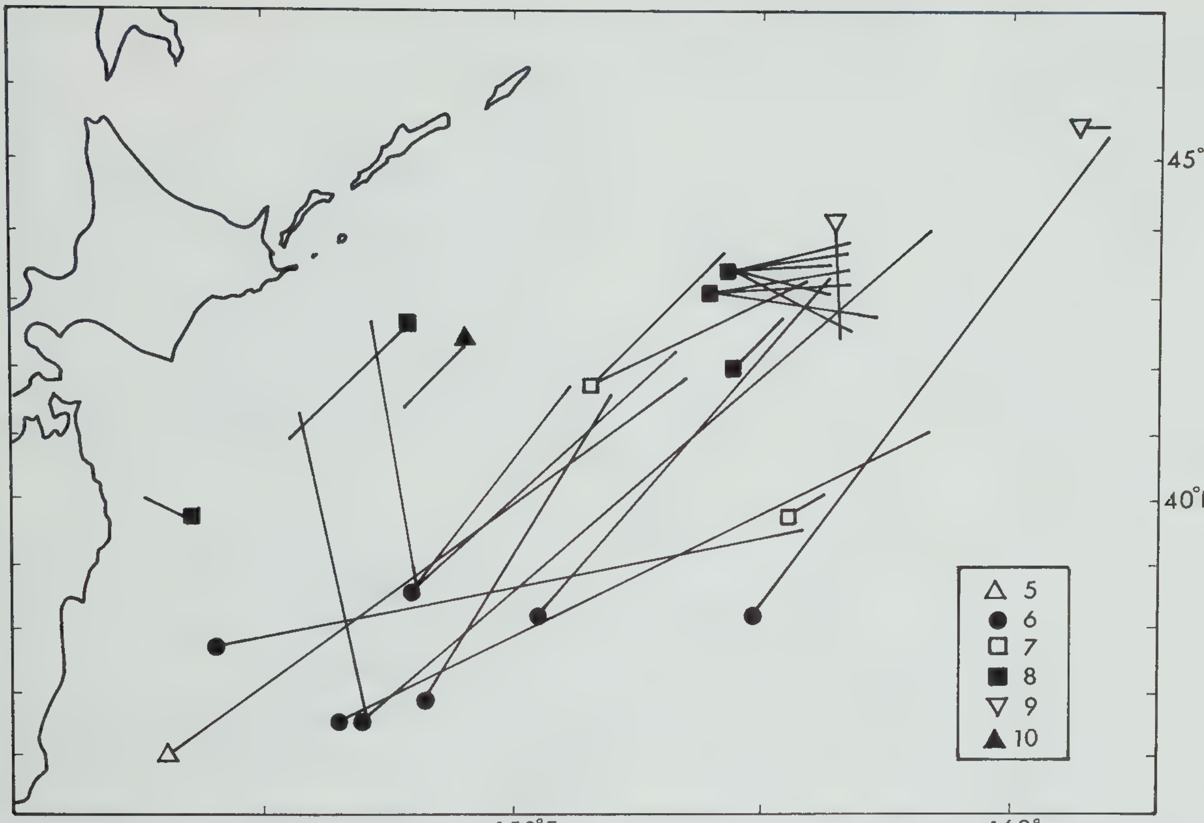


Figure 10. Release and recapture of tagged *Ommastrephes bartrami* in 1977 and 1978. Figures: Month released.

Watasenia scintillans, *Onychoteuthis boreali-japonica*, and a high proportion of cannibalized *Ommastrephes*. The frequency of planktonic crustaceans was low and fluctuated widely between 2-18%. This probably relates to the stage of development, since it was observed that young squid eat a greater proportion than adults. Among the crustacean species were Euphausiacea and *Parathemisto* sp.

Vegetables and plastics, probably dumped overboard from fishing boats, have sometimes been found in the stomachs of *Ommastrephes bartrami* (Table 2).

In conclusion, *O. bartrami* is piscivorous, whereas *T. pacificus* depends principally on plankton.

3. Changes in the resources.

The jig fishery catch of *O. bartrami* in the area west of 170°E rapidly increased until 1978 but declined markedly in 1979. The increase in catch through 1978 was due to the expanded fishing area and increased fishing efforts, whereas the decline in 1979 was due to reduced fishing efforts caused by the steep increase in oil prices, a change in fishing methods to drift gillnets, and an increase in the catch of *T. pacificus* in the Sea of Japan. During the four year period 1976-1979, the catch per unit of effort (CPUE) index, one of the measures used in stock assess-

TABLE 2

Stomach contents of *Ommastrephes bartrami*.

		Stomach contents			
Sampling month		Fish	Squid	Crustacea	Others
1968-1974,	6- 9	59%	24%	18%	– %
1976,	9-10	71	18	10	1
1975-1976, 2,	6-10	76	18	7	—
1977,	1- 3	66	30	2	1
1978,	1- 3	67	20	2	11

Others; vegetables, plastics, etc.

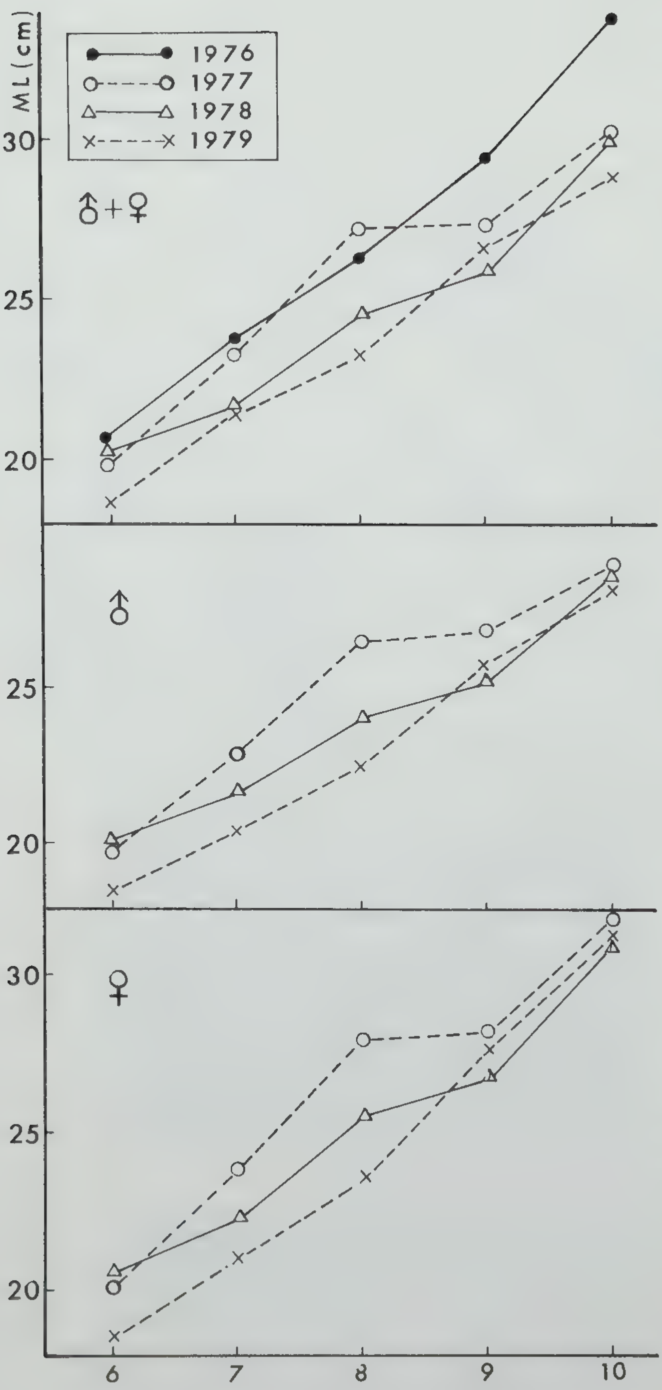


Figure 11. Monthly changes of mean mantle-length of *Ommastrephes bartrami* taken in the sea area west of 160°E in the North Pacific Ocean.

ment, showed its highest value in 1977 and decreased in 1978 and 1979 (Table 3). If one compares 1978 and 1979, CPUE in the former year was slightly higher than the latter (Table 4). Furthermore, the CPUE calculated for every five degrees of longitude and for the size of jigging boat classified as small, medium and large, also significantly decreased in 1979 compared to 1978. The decrease was 10-30% for small boats, 10-40% for medium boats, and 20-40% for large boats (Table 5). While CPUE values are generally higher offshore than in coastal areas, the difference between these two years was larger in the coastal area than in the offshore area.

TABLE 3

Catch per night of a jigging boat in number of cases, about 10 kg each.

	1976	1977	1978	1979
Medium scale fishing boat	191 case	216 case	139 case	147 case
Large scale fishing boat	230	233	217	174

While the total level of resources in these waters can be grossly estimated, it is nearly impossible to calculate absolute numbers in each year because of the lack of complete fishing statistics and ecological information. Nevertheless, we tentatively estimated the amount of the original resource by DeLury's methods using monthly CPUE of medium jigging boats and monthly total catch in the whole fishing area. CPUE and accumulated catch which had been indexed by weight were converted into the number of squid by dividing with average

TABLE 4

Catch per day of a jigging boat.

	Year	Small boat	Medium boat	Large boat
Catch weight kg	1978	759	1 722	2 491
	1979	529	1 347	2 303
Number of squid	1978	1 420	3 330	4 980
	1979	1 140	2 500	5 820

TABLE 5

Catch per day of a jigging boat in each sea area.

Boat scale	Year	−144°E N	−144°E CPUE	145°−149°E N	145°−149°E CPUE	150°−154°E N	150°−154°E CPUE	155°−159°E N	155°−159°E CPUE	160°−164°E N	160°−164°E CPUE	165°−169°E N	165°−169°E CPUE
Small	1978	5	570 kg	2	970 kg	0	1 400 kg	–	– kg	–	– kg	–	– kg
	1979	7	420	2	880	(0)	730	–	–	–	–	–	–
Medium	1978	7	1 190	13	1 630	5	1 990	3	2 290	0	2 020	–	–
	1979	10	770	10	1 390	3	1 670	2	1 990	0	1 770	(0)	2 000
Large	1978	(0)	1 560	1	2 200	3	2 080	4	2 550	4	3 050	–	–
	1979	(0)	1 160	0	1 240	0	1 240	3	2 080	2	2 540	0	3 160

N: Rank of operation days
(0): 1-99, 0: 100-999, 1: 1000-1999, 2: 2000-2999, 3: 3000-3999
The rest is omitted

TABLE 6

Average body weight of *Ommastrephes bartrami*.

Month	Sea area west of 149°E		Sea area west of 159°E		150°-165°E	
	Small scale boat		Medium scale boat		Large scale boat	
	1978	1979	1978	1979	1978	1979
July	205 gr	242 gr	275 gr	270 gr	275 gr	270 gr
Aug.	436	344	414	354	427	330
Sept.	488	479	498	540	641	477
Oct.	920	881	826	703	916	628

TABLE 7

Monthly accumulated catch and catch per day of a medium scale jigging boat.

Month	Monthly accumulated catch by jigger	Monthly accumulated catch by jigger and gill-net	Catch per day a medium scale jigging boat
8	45 (10^6) indiv	45 (10^6) indiv	4 810 indiv
9	123	123	3 160
10	155	167	1 700
11	161	208	1 490

weight per individual (Figure 12). The initial stock recruited into the fishery thus calculated amounted to 219 to 264 million individuals. The catch rate on the other hand turned out to be about 0.8, too high to allow optimism for the future of the fishery.

According to our studies on *O. bartrami*, the monthly average mantle length was largest in 1976 but has been decreasing since 1977. This trend probably is caused by a decline in the number of large squids as shown in Fig. 9 where the lengths of squids caught between August and September are compared for several years. Although a number of factors still remain unknown, a hypothesis to explain this decline in size is described below.

While several populations differing in maturity stage emerge every year, those containing

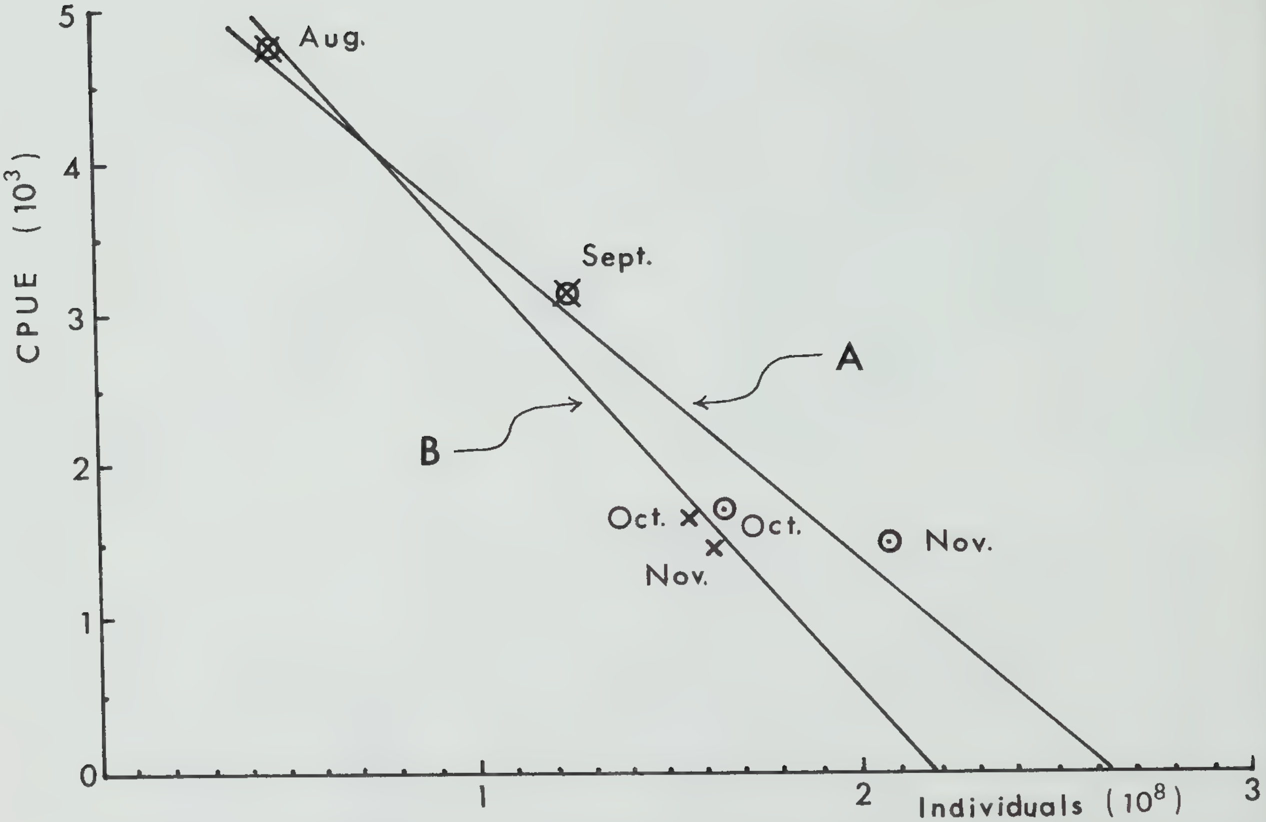


Figure 12. Relation between accumulated catch and average catch per night of a medium scale fishing boat for each month in 1978.
A ⊙: Number of squid caught by both jig and gillnet
B ×: Number of squid caught by jig only.

large squids which are hatched early in the winter-spring spawning period and which grow fast will migrate first into the fishing grounds where they are readily captured. As a result, the rate of squid hatched in spring has gradually increased relative to those hatched in winter. According to this model, the resource is in danger and susceptible to overfishing. Further promotion of fishing effort will severely interfere with reproduction and viability of the resource.

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FISHERY AND BIOLOGY OF *NOTOTODARUS GOULDI* (McCOY, 1888) IN WESTERN BASS STRAIT

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Abstract

Data on the abundance of *Notododarus gouldi* from 134°E to 146°E collected during the 1979/80 squid jigging season is presented. In some areas, the full moon can depress catch rates by as much as 50 per cent. The length-weight relationship for males and females is significantly different, and data on reproductive maturity suggest a protracted mating season.

Introduction

The squid *Nototodarus gouldi* (McCoy 1888) occurs in oceanic and open coastal waters of southern Australia. As yet, its biology, geographic limits and taxonomic affinity to the two New Zealand species *Nototodarus sloani* (Gray) and *Nototodarus* sp. (Smith *et al.*, 1981) are poorly known.

Harrison (1979) described three 'broods' or subpopulations of *N. gouldi* in Tasmanian waters but it cannot be assumed that this will be the situation throughout southern Australia. Kawakami (1976) identified eight subpopulations of *N. sloani* in waters around New Zealand on the basis of size composition, gonad maturity, spawning area and season. Investigations by Smith and co workers (1981) indicated the presence of two species of *Nototodarus*.

Feasibility fishing for *N. gouldi* commenced in the summer of 1978/79, with 19 Japanese squid jigging vessels operating in south east Australian waters (Figure 1). Since catch rates obtained by these vessels were promising, large scale feasibility fishing, involving 63 Japanese and one Taiwanese squid-jigging vessels was undertaken in the summer of 1979/80. Twenty-seven of these vessels operated off South Australia and Victoria in accordance with an agreement to distribute effort throughout the area during the season. Vessels began fishing on December 21, 1979 and concluded on April 6, 1980.

This paper presents the results of fishing by these 27 vessels, with some preliminary observations on the morphometry, reproduction and stomach contents of *N. gouldi*. Such observations will be of value for management of the fishery, and in the identification of distinct subpopulations of the species.

Materials and Methods

Each fishing vessel kept a daily log of its fishing operations, including data on daily catch, hours fished, depth and sea state. Observers on board vessels verified the log book data and collected the following additional data on a daily sample (N = 50) of *N. gouldi*.

Mantle Length: Measured dorsally (to the nearest mm) using a measuring board

Body Weight: Measured to the nearest 10 g using a Salter spring balance.

Sexual Maturity: Recorded for males and females using the index in Appendix I.

Hectocotylisation: Adult males of the genus *Nototodarus* have both ventral arms hectocotylised. Presence of hectocotylisation was recorded for all individuals.

Copulation: Mated females were readily identified by the presence of spermatophores in the buccal region.

Stomach Fullness: Recorded as empty, ¼, ½, ¾, full.

Stomach Contents: Analysed macroscopically with a hand lens (× 10 magnification).

Results and Discussions

Catch Rates: The mean monthly catch rates (kg/hour) by half degree squares for all 27 vessels are shown in Figure 2 for consecutive months from December 1979 to March 1980. The highest catch rates occurred from longitude 136°-141°E in December 1979 and January

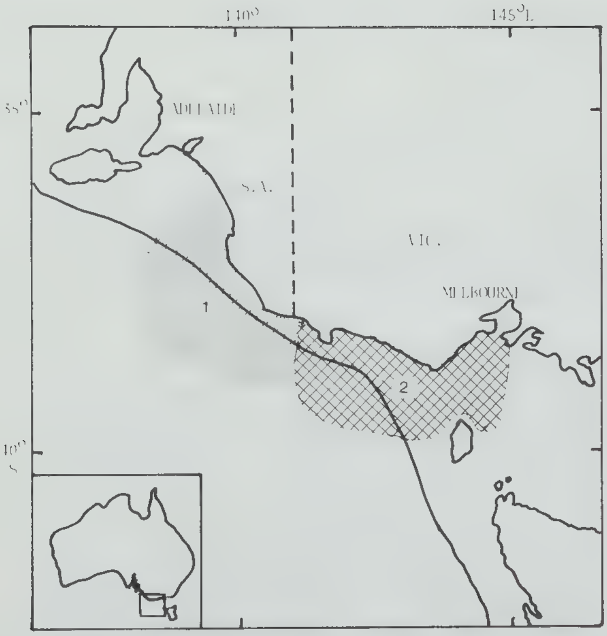

Figure 1. Location of major fishing areas in South Australian (Area 1) and Victorian (Area 2) waters. (Contour line represents the edge of the Continental Shelf.)

1980. In February and March 1980 catch rates declined in this area but increased in the blocks to the south and east in western Bass Strait. Catch rates in the area west of 136°E were low early in the season, and declined to even lower levels as the season progressed, despite a continuing fishing effort of 30 vessel days per month throughout the season.

Using the catch rate as a measure of stock abundance and assuming catchability is constant, the data suggest that the principal stocks occurred in western Bass Strait, with decreasing abundance westerly into the Great Australian Bight. A south-easterly migration into Bass Strait during the season could explain the increased abundance in that region.

Environmental Effects

Lunar cycle:

Areas 1 and 2 (Figure 1) were the only regions in which fishing was conducted continuously throughout the lunar cycle. Plots of mean daily catch rates against time for these regions (Figure 3) show that catch rates are markedly lower around the time of the full moon, although some variability is evident due to differences in catches between vessels. Grouping of the daily catch rate into four weekly periods in relation to the lunar cycle (Table 1) shows that during the week of the full moon catch rates are nearly 50 per cent lower in Area 1 and about 25 per cent lower in Area 2 than in any other week. A relationship between catch rates and the full moon in a squid jig fishery has been demonstrated for *Illex illecebrosus* by Ichikawa & Sato (1976) and for *N. gouldi* by Ichikawa (1978).

The high variability in catch rates both in time and place (Figure 3) may be due to a tendency for *N. gouldi* to school, as is the case with many species of pelagic squid (Bennett, 1978).

Depth: N. gouldi was generally taken in neritic waters over the continental shelf. Table 2, giving total catches according to depth for Areas 1 and 2, shows that a greater proportion of the catch was taken in somewhat deeper water in Area 1 than in Area 2. However, in the regions showing the greatest abundance of squid, the continental shelf break (177 m depth contour) occurs closer to shore in Area 1 than in Area 2 (Figure 1). Since vessels were excluded from State territorial waters (i.e. within 3 nautical miles of the coast), it is possible that these differences in catch rate according to depth are a result of greater fishing effort in deeper water in Area 1.

Biological Data

Length-Weight Relationship:

Least square regressions were calculated for length and weight data for *N. gouldi*, and gave the following equations.

Males W $= 0.0139\ L^{3.2128}$ ($N = 4723$; $r^2 = 0.91^{***}$)

Females W $= 0.0392\ L^{2.869}$ ($N = 3311$; $r^2 = 0.92^{***}$)

Combined Sexes W $= 0.0279\ L^{2.9878}$ ($N = 8034$; $r^2 = 0.92^{***}$)

where W = fresh weight and L = mantle length.

The slope of the regression calculated for males was found to be significantly different from that for females ($t = 17.0$, $p < 0.05$).

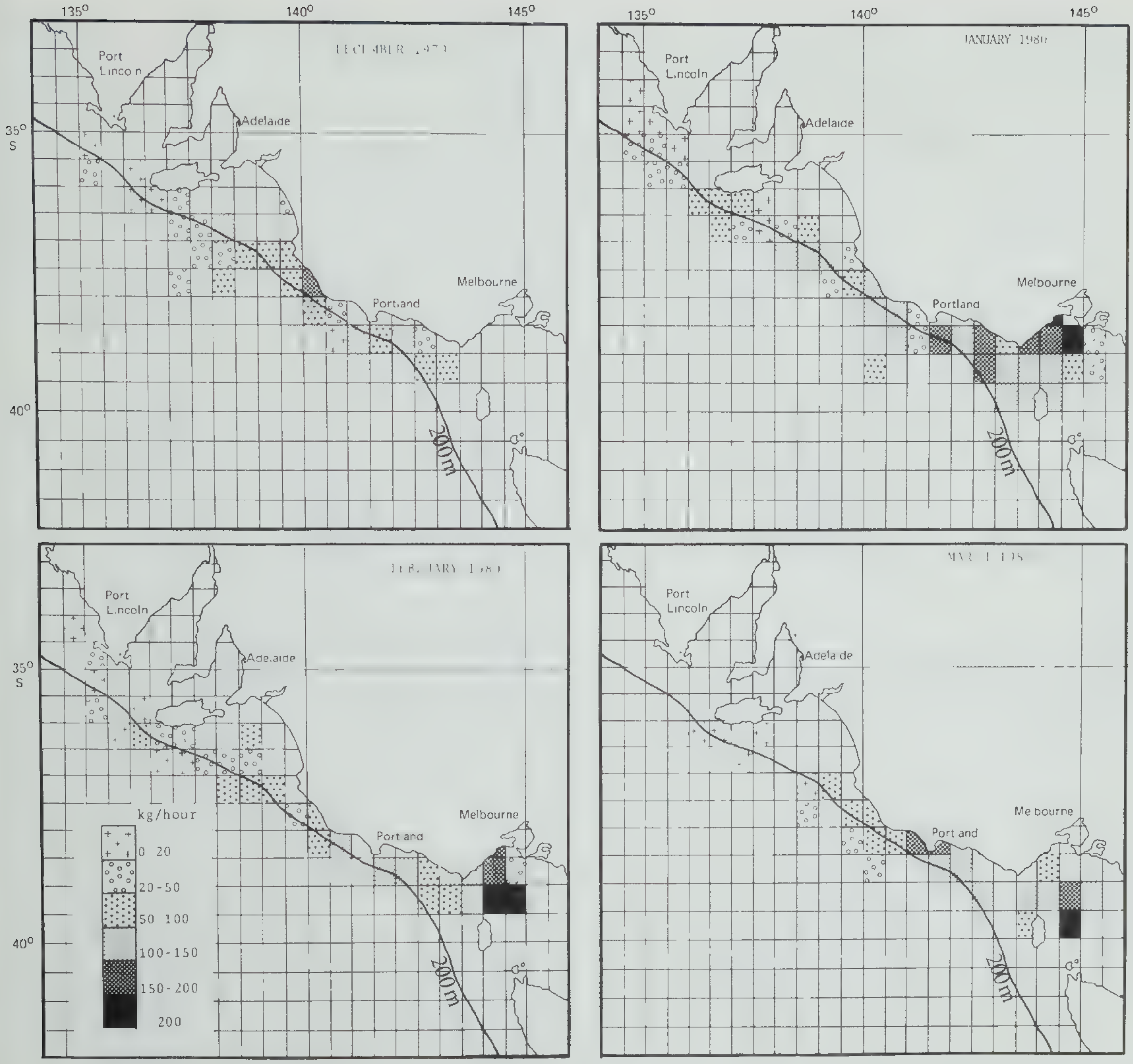

Figure 2. Catch per unit effort (kg/hour) by half degree square December 1979 to March 1980.

TABLE 1

Average catch rate (kg/hr) with respect to lunar phase for Areas 1 and 2, January 1980 to March 1980.

	AREA 1				AREA 2			
	Jan.	Feb.	Mar.	Average	Jan.	Feb.	Mar.	Average
Last Quarter	108	81	99	95	202	136	197	181
New Moon	123	103	107	112	162	164	141	157
1st Quarter	144	74	111	114	168	167	123	156
Full Moon	39	67	45	51	138	135	82	129

TABLE 2

Total catch of squid at different depths for Areas 1 and 2 during the 1979/80 season.

	AREA 1		AREA 2	
Depth (m)	Quantity (tonnes)	%	Quantity (tonnes)	%
50	0	0	<0.1	<0.1
51-70	40.1	5.1	265.6	15.7
71-90	277.3	35.0	1100.9	65.4
91-110	285.3	36.0	297.2	17.6
111-130	132.8	16.8	16.8	1.0
131-150	43.6	5.5	3.7	0.2
150	12.7	1.6	0	0

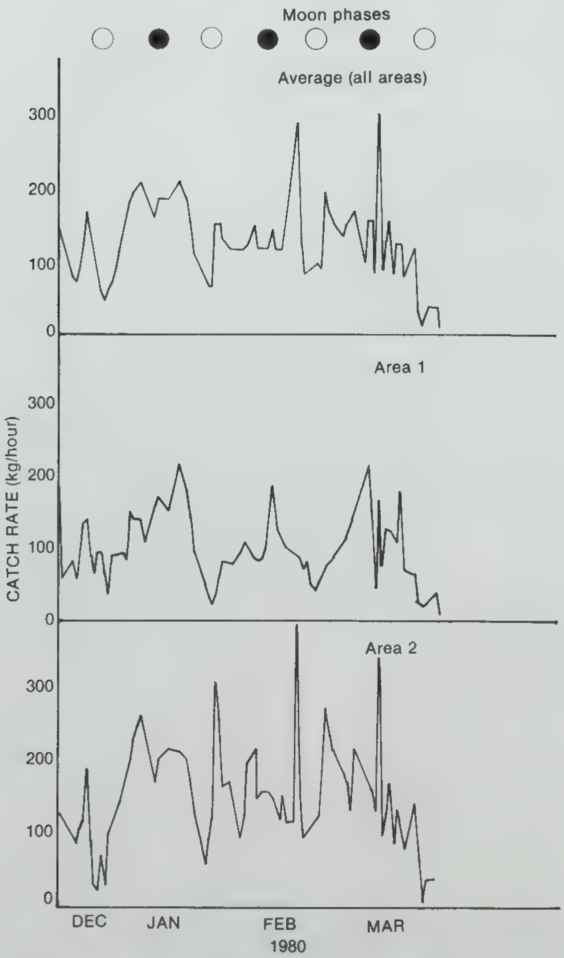

Figure 3. Relationship between lunar phase and daily catch rate for Areas 1 and 2, December 1979 to March 1980. (Open circles represent full moon, closed circles represent new moon.)

A plot of length against weight for the sexes (Figure 4) shows that males are heavier for a given length. However, females grow to a greater maximum size. Similar differences between the sexes have been recorded by Harrison (1979) for this species in Tasmanian waters and by Lange & Johnson (1981) for *Loligo pealei* and *Illex illecebrosus*. This relationship may differ with area and time for a particular species (Lange & Johnson, 1981), and thus be of value in distinguishing between different subpopulations of this species.

Reproductive Maturity: Details on reproductive maturity are shown in Table 3. The percentage of mated females correlates well with the percentage of mature females ($r^2 = 0.82$***) and to a lesser extent with percentage of mature males ($r^2 = 0.54$***). Males exceeded females in number throughout the season. There are no obvious trends in maturity; mature males and females are present throughout the season, suggesting a protracted mating season.

All half mature and fully mature males exhibited hectocotylisation, with the minimum

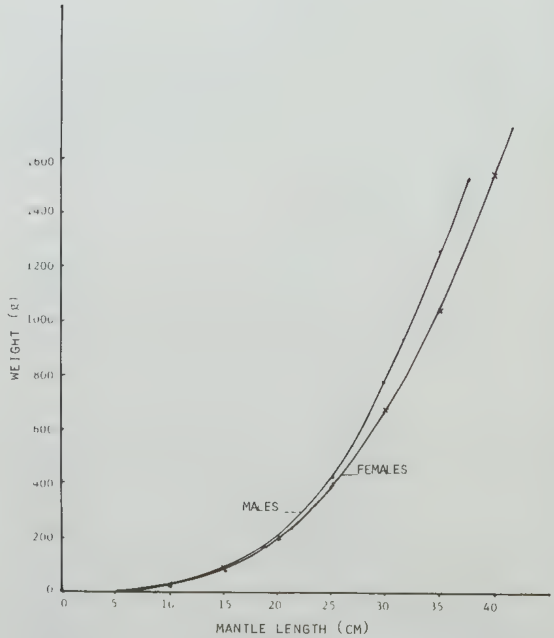

Figure 4. Relationship between dorsal mantle length and total live weight for male and female *N. gouldi*.

TABLE 3

Data on reproductive maturity and male/female ratios per week for Areas 1 and 2, December 1979 to April 1980.

DATE	% MATED FEMALES		% MATURE FEMALES		%MATURE MALES		M:F RATES	
	AREA		AREA		AREA		AREA	
	1	2	1	2	1	2	1	2
21/12-27/12	64.4	–	71.8	–	79.5	–	1.26	–
28/12-3/1	59.8	–	56.8	–	81.7	–	1.58	–
4/1-10/1	22.4	–	29.9	–	53.5	–	1.42	–
11/1-17/1	27.9	55.8	23.7	55.8	45.5	90.7	1.21	1.21
18/1-24/1	75.0	81.7	72.2	74.4	90.7	90.1	2.37	1.87
25/1-31/1	–	–	–	–	–	–	–	–
1/2-7/2	–	–	–	–	–	–	–	–
8/2-14/2	57.9	86.7	59.6	86.7	77.7	92.0	1.31	1.73
15/2-21/2	64.2	51.2	63.3	48.8	94.4	100.0	2.79	1.58
22/2-28/2	79.9	21.0	91.6	–	100.0	–	2.1	1.5
29/2-6/3	51.4	25.7	46.0	13.4	86.7	58.5	1.55	1.54
7/3-13/3	90.9	32.8	71.8	37.3	79.0	52.6	1.5	1.12
14/3-20/3	86.3	43.9	62.6	55.3	81.8	78.8	1.88	1.18
21/3-27/3	–	72.0	–	76.7	–	91.7	–	1.46
28/3-3/4	77.0	–	–	–	–	–	0.92	–
4/4-10/4	–	–	–	–	–	–	–	–

size at hectoctoylisation being 14 cm mantle length.

Analysis of Stomach Contents: Crude analysis of stomach contents on 920 individuals gave the following components.

squids (Ommastrephidae)	57%
fishes (primarily pilchards)	42%
other	1%

The large component of squids in the gut may be an artefact of the fishing operation since squid jigging is reported to induce a 'feeding frenzy' among squid, resulting in a high degree of cannibalism (Bennett, 1978; Merdsoy, 1978).

Conclusions

Feasibility fishing has indicated the presence of considerable numbers of *N. gouldi* in south east Australian waters. Victorian waters were more productive than South Australian waters during the months January to March with populations apparently moving southerly and easterly during the season. Catches were predominantly in neritic waters over the continental shelf. Catch rates were markedly affected by the lunar cycle, the magnitude of which differed between areas. No differences in reproductive state were found with time or with place indicating a protracted mating season. The length-weight relationship for the species within the study area was significantly different for males and females.

Acknowledgements

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Appendix I

Males

Immature: Vas deferens invisible; testes small, soft and clear; no spermatophores; hectocotylus difficult to distinguish.

Half Mature: Vas deferens invisible or small; testes longer, firmer and less transparent; spermatophores small, usually visible; hectocotylus readily distinguished.

Mature: Vas deferens white and ridged; testes large and white with central ridge; some spermatophores usually ejaculated into mantle cavity; Needham's sac full and large; hectocotylus obvious.

Females

Immature: Oviduct glands not visible; nidamental gland small, thin and transparent—almost imperceptible; ovaries small, clear and soft; oviduct small.

Half Mature: Oviduct glands larger—'Squiggles' obvious; nidamental glands longer and thicker, whitening; ovaries whitening; oviduct not obvious.

Mature: Oviduct glands large, translucent brown/yellow, containing visible eggs; nidamental glands large, thick and white; ovaries cream colour with visible eggs; oviduct white and obvious.

A BRIEF REVIEW OF THE SQUID SURVEY BY HOYO MARU No. 67 IN SOUTHEAST AUSTRALIAN WATERS IN 1979/80

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Abstract

The Japan Marine Fishery Resource Research Center (JAMARC) carried out the Gould's squid, *Nototodarus gouldi*, resource survey in conjunction with the Australian fisheries authorities, using the commercial jigging boat Hoyo Maru No. 67, in southeast Australian waters between November 1979 and April 1980. This programme was the third year of the Japanese Fisheries Technical Assistance to the Australian Commonwealth. The major purpose of the survey was to develop the Gould's squid resource on a commercial scale and to collect biological information about squid and oceanographic data on the fishing ground.

Catch

The catch distribution of the *N. gouldi* for the 1979/80 season is shown in Figure 1. During the 117 days fished, a total of 43.7 tons of the *N. gouldi* was caught (Table 1). Only 14 squids of the pelagic species *Todarodes filippovae* were taken incidentally off the east coast of Tasmania. Of the total catch 42.4 tons came from 117 usual night-time fishing stations and only 1.3 tons were caught during 22 experimental daytime operations. Quantities of squid caught by month rose from 3 tons in November to 12.6 tons in February, fell to 10.8 tons in March, and further to 5 tons in April. The bulk of the catch was obtained in February and March. The catch per unit effort also increased steadily through the season, peaked in February and fell in March. Figure 2 shows the distribution of the catch per unit effort.

A total of 20 tons—almost half the season's catch—was taken in the western part of the Bass Strait in 51.5 fishing days. The other significant ground was the continental shelf between Capes Otway and Northumberland. Here 11.6 tons were produced in 20 fishing days and the catch rate was about 0.6 ton per day fished. This area also contributed to the joint feasibility fishing survey in South Australian and Victorian waters in 1979/80 season.

Hand jigging was observed to have been efficient in southeast Australian waters and the squids jigged by hand were large and sexually mature. Another noteworthy character of fishing for *N. gouldi* in the area concerned is that there were few cases of an intensive catch of squid in a short time, as has been experienced very often for the New Zealand common squids, *Nototodarus* spp.

Environmental Factors

Wind: Fishing efficiency is diminished through high wind-induced waves and swells when the wind exceeds force six on the Beaufort scale. It was rather windy in the southeast region of Australia in the 1979/80 season. One fishing day was lost in November, five in December, one in February and one in March because of rough weather.

Water temperature: Surface water temperatures of 14° to 18°C were distributed in southeast Australian coastal waters throughout the season. The temperature of the 1979/80 season was lower by about 1° to 2°C than in the previous season. The thermocline observed during the season, especially in the Bass Strait, was not as well developed as the one in the 1978/79 season, while a conspicuous thermocline was distributed on the continental shelf west of Cape Otway.

Body Length

Females seem to grow about 5 cm larger than males. The jigged females range from 10 to 40 cm mantle length, while males range from 10 to 35 cm mantle length. Figure 3 shows length frequency distributions of squid by month throughout the area surveyed. Although a population for a summer fishery was clearly defined, grew steadily through the season, and

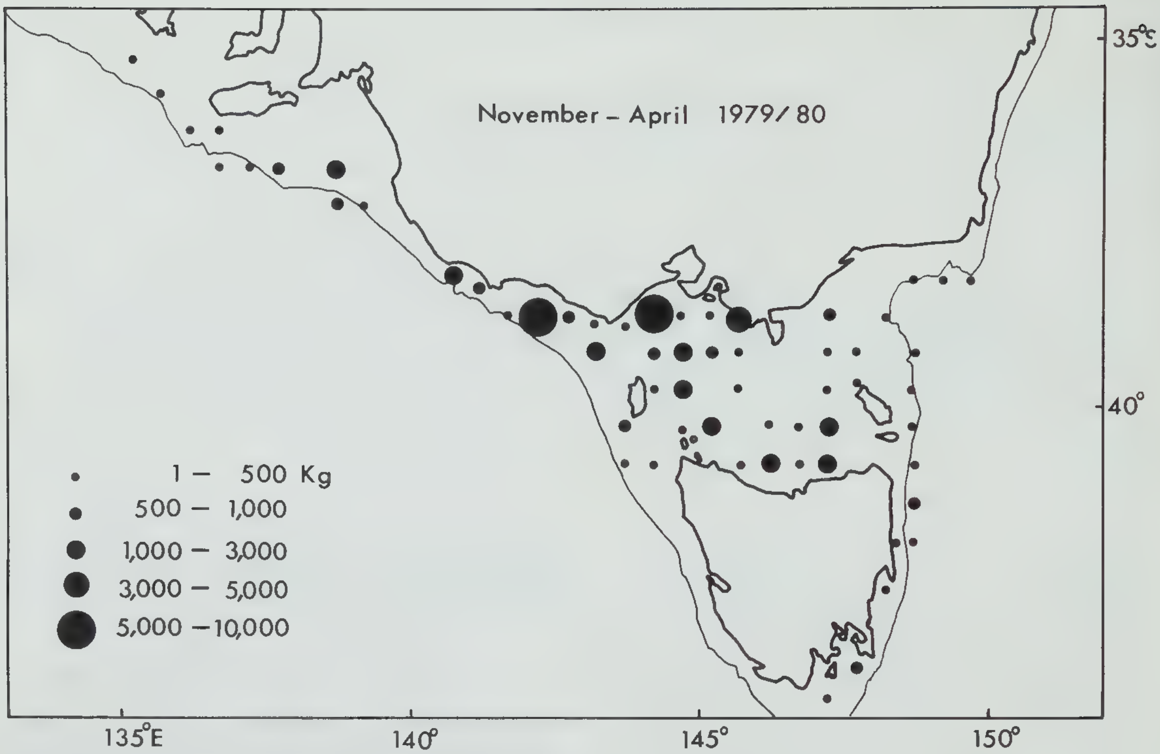

Figure 1. Catch of Gould's squid, *Nototodarus gouldi*.

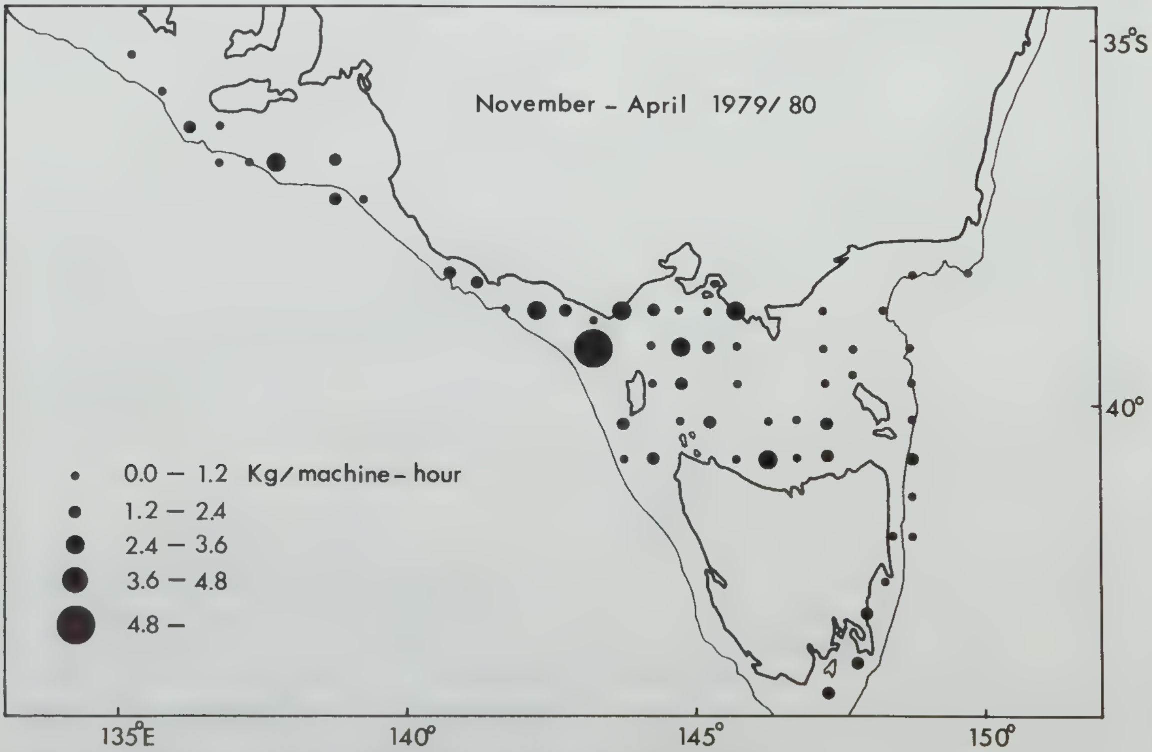

Figure 2. Catch per unit effort (excluding the daytime experimental catch).

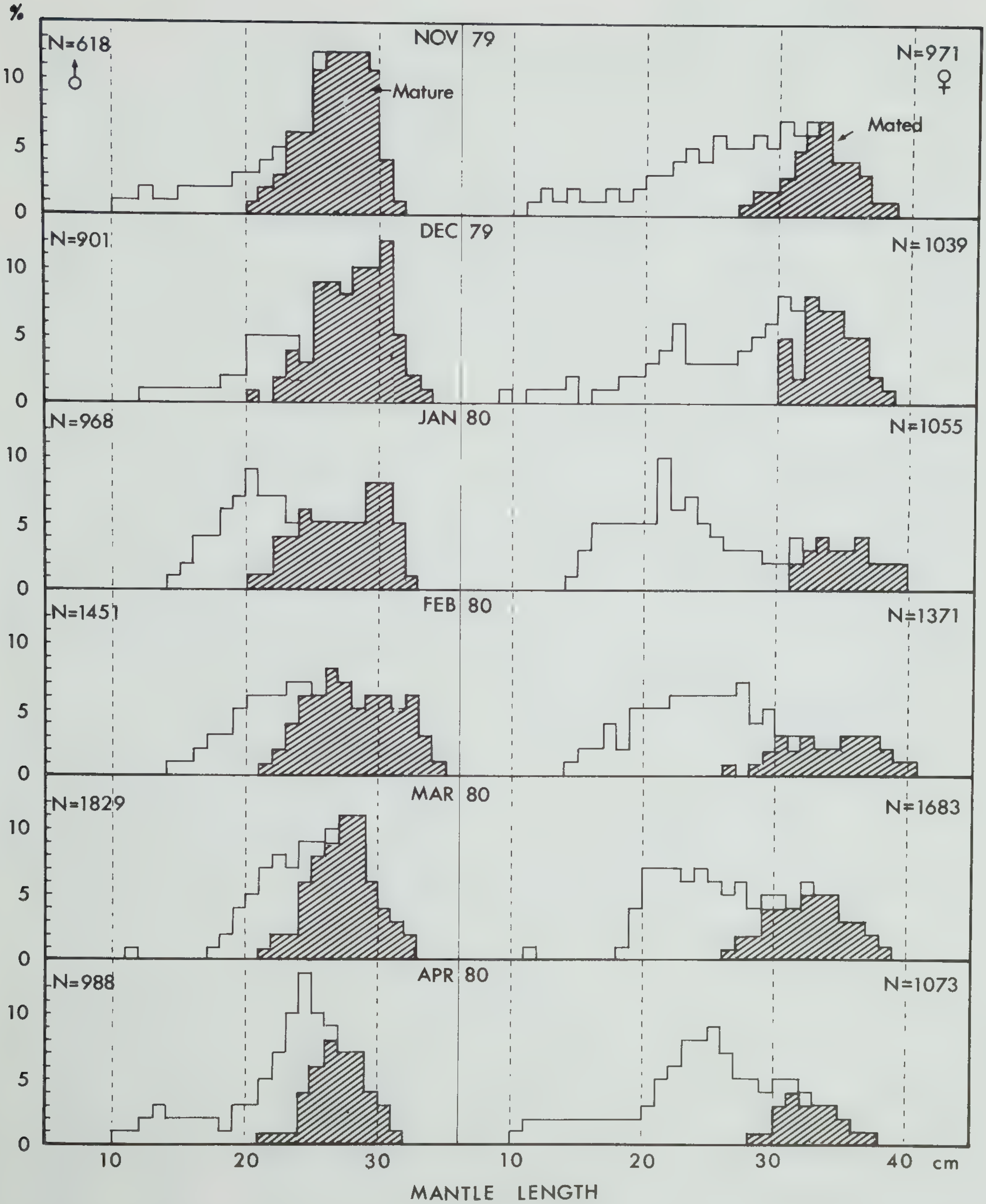

Figure 3. Length frequency distribution of squid, Nov. 1979-Apr. 1980.

appeared to have spawned from February to March in the 1978/79 season, the length frequency distribution of squid and their sexual stages in the 1979/80 season did not reveal a similar trend.

The major component of a population caught in November to December consisted of rather large and mature squids: bigger than 25 cm in males and 30 cm in females. The large, mature squids may have been a brood from the previous spring which would have been too late for spawning in relation to some oceanographic condition. The low water temperature during the summer may be related to a reduced growth of a population for the season's fishery, probably in the autumn to winter brood.

Althouth the greatest percentage of mature males and some mated females was caught between January and April, a slight tendency of growth during other months of the season was observed. In March the small squids less than 15 cm in mantle length were recruited into the fishery. These small squids seem to have been the spring brood of the season.

The monthly change of length frequency distribution of squids and the occurrence of mature males and mated females throughout the season suggest that the spawning ground was very broadly distributed over southeast Australian coastal waters.

Stomach Contents

Fishes, crustaceans and squids were the principal food items of the squid. The fishes included the herring-like fishes, juvenile barracutas, and garfishes. Shrimps, shrimp-like crustaceans and megalopa larvae of crabs were important in the crustacean food category. Juvenile squids eaten seem to be *N. gouldi*. The spermatophore sacs without spermatophores sometimes were found in stomachs of mated females, as were scraps of food discarded from the ship.

On the other hand, *N. gouldi* is eaten by barracoutas, red snappers, flatheads, scads, gurnards, gurnard perches, and presumably by fur seals and dolphins. Fur seals, barracoutas, and sharks often broke the jigging lines when they attacked jigged squids.

Movement and Growth

A total of 2 266 squids was tagged and released at ten localities. Four squids were recaptured by the feasibility fishing boats during the season (Table 2). Their movement had a westward component.

The growth of the squid with tag J33 is conservatively estimated at 3 cm mantle length for 35 days, while growth of the squid with tag J53 was estimated at least at 1 cm for 28 days.

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TABLE 1

Catch, fishing effort and catch per unit effort (excluding daytime experimental fishing).

	1979		1980				
	Nov	Dec	Jan	Feb	Mar	Apr	Total
Days	19	19	17	23	25	14	117
Hours	171	150	135	209	232	146	1 044
Machine-hours	4 124	3 607	3 167	5 125	5 426	3 619	25 066
Catch (kg)	3 096	5 627	5 226	12 620	10 844	4 953	42 366
Catch/day (kg)	163	296	307	549	434	354	362
Catch/hour (kg)	18	38	39	60	47	34	41
Catch/machine-hour (kg)	0.8	1.6	1.7	2.5	2.0	1.4	1.4

TABLE 2

Squids tagged, released and recaptured.

Mark	Tagged and Released				Recaptured			
	Date	Location	No.	M.L. (mm)	Date	Location	No.	M.L. (mm)
J33	13 Jan 80	38°51'S 145°41'E	525	170-230	17 Feb 80	39°46'S 144°37'E	1	260
J48	7 Feb 80	36°57'S 138°48'E	105	250-300	10 Feb 80	37°02'S 138°12'E	1	270
J49	8 Feb 80	36°58'S 138°46'E	210	220-280	14 Feb 80	37°01'S 138°21'E	1	245
J53	3 Mar 80	38°58'S 145°33'E	315	200-250	31 Mar 80	39°09'S 144°45'E	1	260

THE BIOLOGY OF JIG-CAUGHT ARROW SQUID (*NOTOTODARUS* SPP.) IN NEW ZEALAND WATERS

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Abstract

Two species of *Nototodarus* occur in New Zealand waters. They are caught by jigging from December to May. *N. sloani* is found in northern (warmer) waters; while *Nototodarus* sp. occurs in southern (colder) waters. Growth rates for both species are 2.5-4.0 cm ML per month for younger squid, and 1.5-3.0 cm ML per month for older squid, with a total life span of at least 12 months. Possible spawning grounds are inferred from presence of mated females. The general ecology is discussed.

Taxonomy

Nototodarus sloani (Gray, 1845) was described from specimens collected in Waitemata Harbour off the north-east coast of New Zealand (36°40′S latitude). *Nototodarus sloani* is distributed north of the subtropical convergence zone and is replaced by an undescribed species of *Nototodarus* which has its centre of distribution within and south of the convergence zone. The two species can be easily distinguished by examination of the male hectocotylised ventral arms (see Smith *et al.*, 1981).

Current studies indicate that *N. sloani* has geographically distinct large and small growth forms. Arrow squid of both sexes from western New Zealand, mature at 26-35 cm ML (maximum mantle length 42 cm) and fully ripe females weigh up to 1800 g, while those from north-east New Zealand mature at 20-25 cm ML (maximum 32 cm) and fully ripe females weigh up to 600 g. The undescribed arrow squid from south and south-eastern waters is similar in growth characteristics to the western population of *N. sloani.*

The jig fishery

In New Zealand coastal waters, arrow squid are caught by traditional Japanese jig fishing methods. Vessels of 99-500+ gross registered tonnes, with between 50 and 80 2000-4000 watt lamps are used with a mix of hand and automatic jigging machines.

Annual catches of both species of arrow squid range between 13,000 and 40,000 tonnes. The vessels usually fish a 90-120 day season between December and April with mean catch rates of 1.5-3.9 tonnes per vessel-day (Table 1). Catch rate varies with vessel size. In the 1978-79 season catch data from 57 vessels showed that CPUE was highest for vessels of 400-499 GRT (Table 2), although the 99 t vessels also had high catch rates.

The jig vessels fish throughout central and southern New Zealand waters but tend to concentrate in specific areas which are becoming traditional fishing grounds. The main fishing areas are evident in the summaries of catch (Figure 1).

Growth rate

Time series of mantle length frequency groups present a confusing picture comprising a mix of modal groups at any one time and no clear indication of consistent increase in one mode in one area. Analyses of about 150,000 measurements (Figures 2, 3) from jigging vessels fishing the 1978-79 season indicates that within the exploited length range both *N. sloani* and *Nototodarus* sp. have similar growth rates of 2.5-4.0 cm ML per month for smaller squid (18-24 cm, 200-400 g) and 1.5-3.0 cm ML per month for larger squid (24-33 cm, 400-900 g).

From these data it is inferred that arrow squids of the two species increase from 18 cm to 28 cm in males and to 33 cm in females in 4½-8 months.

The length-frequency graphs also indicate similar growth rates for very large arrow

TABLE 1

Catch (tonnes) and Catch Per Unit Effort (tonnes per vessel day) of Arrow Squid Caught by Japanese, Taiwanese, and Korean Jigging Vessels 1972-80 in New Zealand Waters

	1972/73	1973/74	1974/75	1975/76	1976/77	1977/78	1978/79	1979/80*
No. vessels	72	157	154	138	135	130	174	182
No. days	3 452	9 605	11 939	12 918	12 437	10 900	16 440	16 074
Total Catch	13 532	14 856	19 201	20 977	26 296	41 750	24 524	40 300
CPUE	3.92	1.55	1.61	1.62	2.11	3.83	1.49	2.51

* Figures for this year preliminary.

TABLE 2

Variation in catch and catch rate (CPUE) of squid for 57 jig fishing vessels during the 1978-79 squid season

Vessel size	No. vessels	Catch (t)	CPUE (t/day)
< 100 t	9	1 184	1.45
100-199	1	75	1.29
200-298	23	2 328	1.13
300-399	10	1 350	1.33
400-499	10	1 912	1.83
500 +	4	332	1.04
	57	7 203	1.35

squids, with the maximum size of males increasing from 27.5 to 34.5 cm ML in 100 days (2.1 cm per month), and for females from 29.5 to 40.5 cm ML in 100 days (3.0 cm ML per month).These data indicate that over the exploited size range arrow squid grow from 18 to 35 cm (male) or to 40 cm (female) in approximately 7½ to 11 months, suggesting a total life span of greater than 12 months.

The stock of *N. sloani* occurring off the north-east of New Zealand, as yet unexploited by the foreign jig fleet, has quite different growth characters from those of *N. sloani* of the west coast stock. The north-eastern squid mature at a smaller length and weight, but like the other stocks appear to have at least two spawning seasons (summer and winter). Insufficient data exist from which growth rates can be described for this stock.

Spawning groups

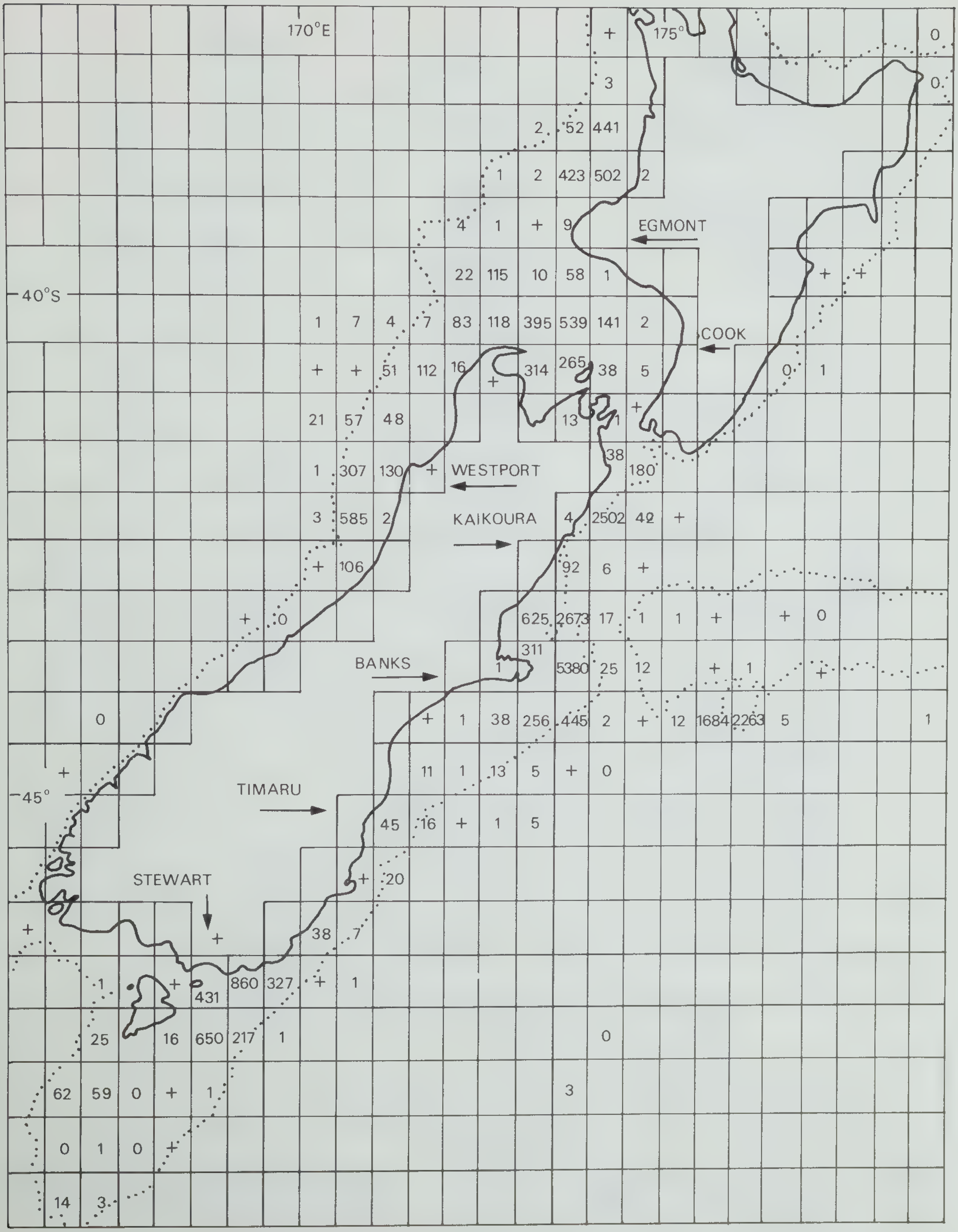
The mantle length frequency graphs (Figures 2, 3) also show that small squid (i.e. "juveniles" < 18 cm mantle length) were frequently caught. In Cook Strait (western New Zealand) *N. sloani* (Figure 2, centre) juveniles were abundant in late December and mid-March, while off Banks Peninsula (eastern New Zealand) *Nototodarus* sp. juveniles were abundant in catches during January and April. These data suggest that at least two spawning groups support the stocks of each species.

The occurrence of a large proportion of mated females (i.e., those implanted with spermatophore sacs around the buccal mass) was used as an indication of possible spawning grounds of arrow squid. In the western waters *N. sloani* apparently has a major spawning in April, probably in the Egmont region where most females over 26 cm ML were implanted with spermatophores from March to mid-May (Figure 2, left). There was no similar indication of a spawning ground for east coast squid (*Nototodarus* sp.) (Figure 3). (Note: subsequent trawl data suggest at least two spawning periods in the Banks region: July and December).

Ecology

Sea surface temperature and salinity data collected by observers during the 1978-79 season have been compiled by 10 day time periods and 0.5° squares of latitude and longitude (Table 3). These data show that squid are caught over a wide range of temperature and salinity values. Catch rates (CPUE) were higher in colder, low salinity water, perhaps reflecting the higher abundance (or catchability) of *Nototodarus* sp. over *N. sloani* during the 1978-79 season.

Figure 1. Catch (tonnes) of arrow squid by 0.5° squares of latitude and longitude for the 1978-79 jig-season (174 vessels, 16, 440 vessel-days, 24,524 tonnes).


170°E
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WESTPORT
KAIKOURA
BANKS
TIMARU
STEWART

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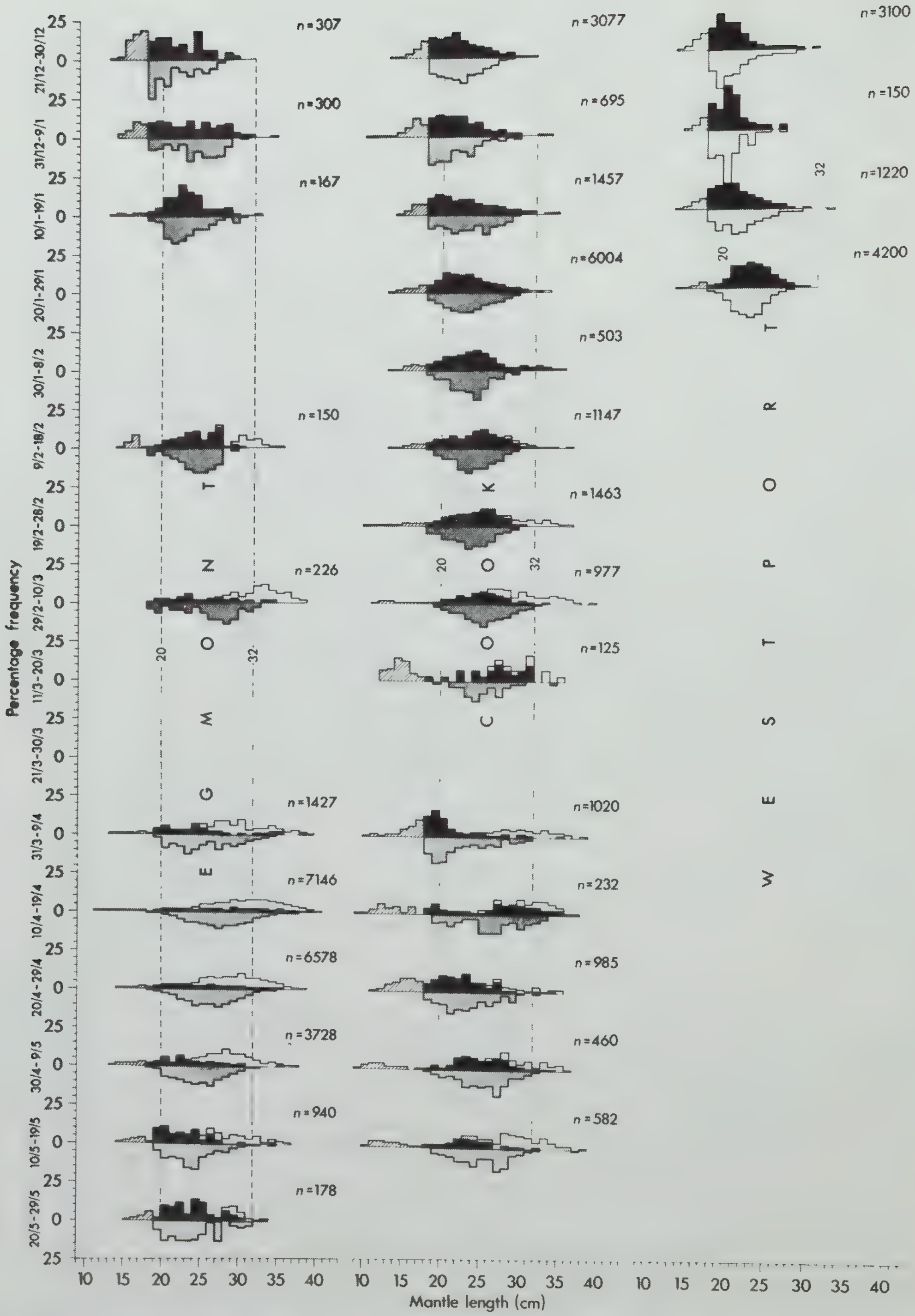

Figure 2. Mantle length-frequency graphs for *N. sloani* during the 1978-79 fishing season by 10-day fishing periods and major fishing grounds (Egmont, Cook, West-port). Hatched areas indicate unsexed specimens, black areas indicate uncopulated females, white areas indicate copulated females and grey areas (below lines) indicate males.

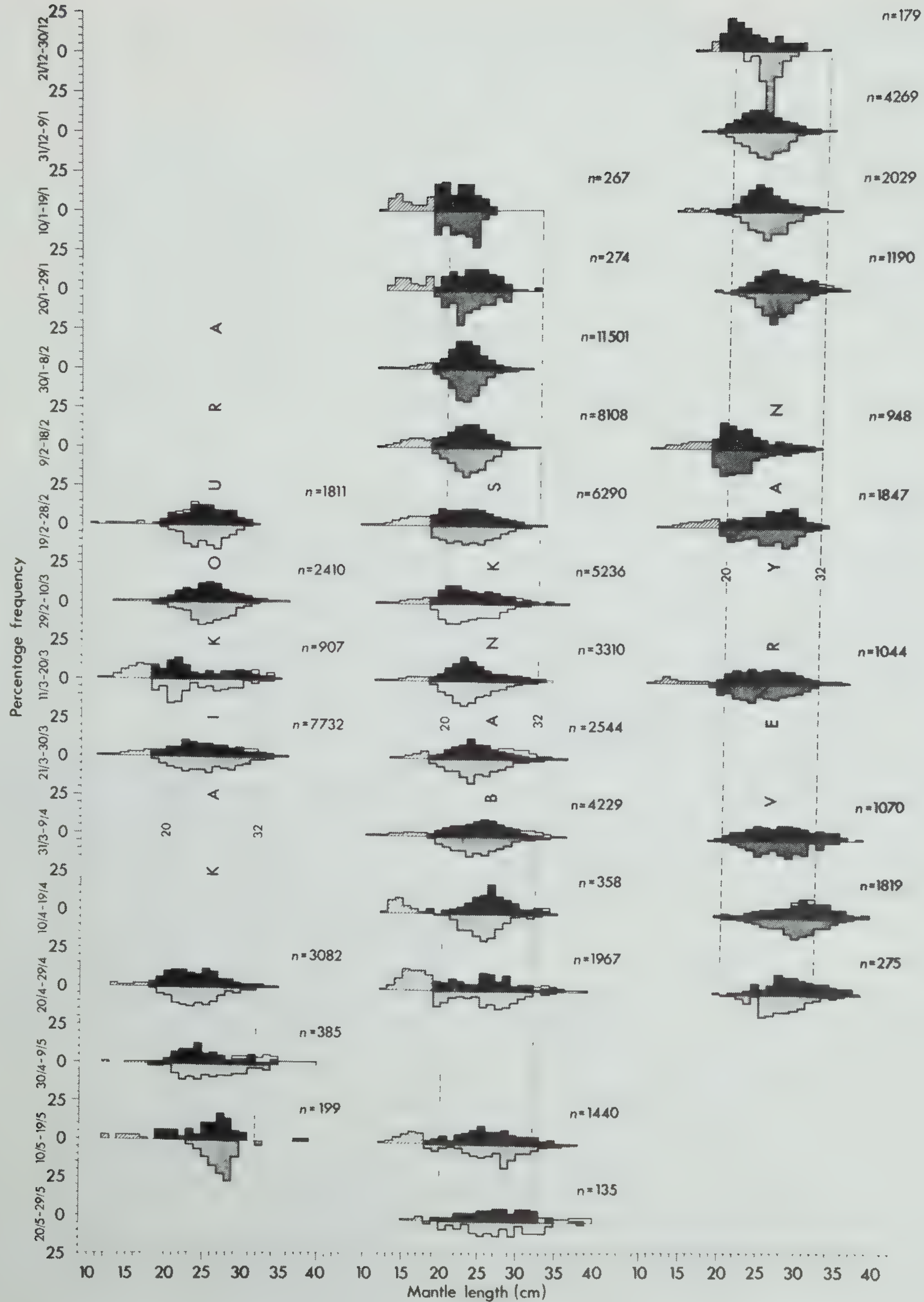

Figure 3. Mantle length-frequency graphs for *Nototodarus* sp. during the 1978-79 fishing season by 10-day fishing periods and major fishing grounds (Karkoura, Banks, Veryan). See Fig. 2 legend for key.

Table 3

Ranges of mean sea surface temperature and salinity data collected on squid-jigging vessels during the 1978-79 squid season

Fishing Area	Temperature (°C) Max.	Min.	Range	Salinity (‰) Max.	Min.	Range
WEST COAST						
Egmont	19.0	16.8	(2.2)	35.26	34.96	(0.30)
Cook Strait	18.5	15.0	(3.5)	35.28	34.65	(0.63)
Tasman Bay	18.4	16.0	(2.4)	35.10	34.63	(0.47)
Westport	19.7	14.7	(5.0)	35.42	33.17	(2.25)
EAST/SOUTH COASTS						
Kaikoura	16.5	11.9	(4.6)	34.64	34.21	(0.43)
Banks Peninsula	16.4	12.0	(4.4)	34.68	34.25	(0.43)
Veryan Bank	15.2	13.5	(1.7)	34.60	34.41	(0.19)
Timaru	16.3	12.6	(3.7)	34.85	34.25	(0.60)
Stewart Island	14.1	12.7	(1.4)	34.83	34.58	(0.25)

Within each species area there was no correlation between CPUE and any particular temperature or salinity range.

Throughout the fishing season the highest catches were made for both species within the depth range 50 to 150 m, where most of the effort was concentrated. There was little effort expended outside this depth range. However, occasional searching by a few vessels in areas further offshore resulted in very high catch rates (Figure 1).

Initial analysis shows that catch rate was independent of both wind speed and wind direction. Vessels fished up to wind force 8 (Beaufort scale) without apparent detriment to CPUE.

Discussion

The fishery for arrow squids is widespread in New Zealand coastal waters, is concentrated along the mid-outer continental shelf region and operates independently of weather conditions. In western waters the jig fishery for *N. sloani* occurs in areas of warmer temperature and higher salinity along the mixing zone between oceanic subtropical surface water and neritic water, while in south-eastern waters the jig fishery for *Nototodarus* sp. operates in colder low salinity waters of the Southland current and subtropical convergence zone (Figure 4).

Recent satellite images of the Cook Strait region show that in January-February 1981 the squid fleet was located along the outer boundary of an area of wind-induced upwelling and nutrient enrichment west and north-west of Cape Farewell (north-west South Island). This upwelling occurs regularly (*see* Roberts, 1977; Roberts & Paul, 1978). Future studies will be directed at investigating the significance of this upwelling area in the life cycle of *N. sloani*.

Acknowledgements

Thanks are due to the observers from Fisheries Research Division, Wellington and to commercial fishermen who made observations on board Japanese jig-vessels. This work would not have been possible without the aid of New Zealand companies involved in cooperative-fishing ventures with the Japanese fishing fleet. I especially thank Mr. S. Canning and Mr. B. Lovell, Fisheries Research Division, Wellington for analysis of log-book data.

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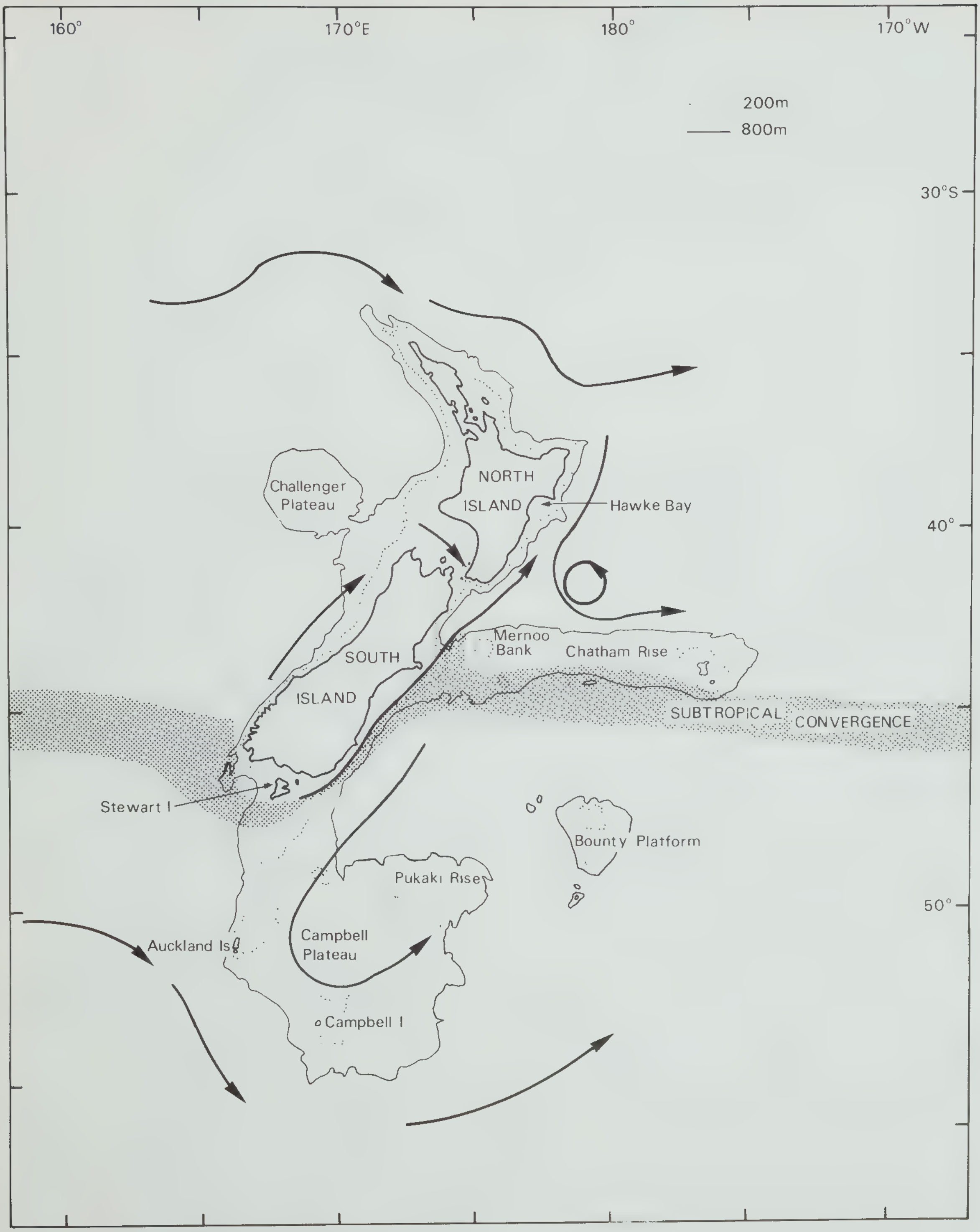

Figure 4. Major bathymetric features and surface currents of the New Zealand region.

SUMMARY OF THE FISHERY AND BIOLOGY OF THE JUMBO SQUID (*DOSIDICUS GIGAS*) IN THE GULF OF CALIFORNIA, MEXICO[1]

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Introduction

The Giant or Jumbo squid, *Dosidicus gigas*, is one of the most abundant of all cephalopod resources in western Mexican waters. A large fishery based on this species has developed in the last three years mainly in the Gulf of California. Existing knowledge about the biological characteristics and exploitation of this species is very limited. Thus an extensive research program to define the taxonomy, biological and ecological characteristics, stock size and exploitation effects was established in 1979. The preliminary results presented here are those generated by analyses of exploratory data as well as commercial statistics. A summary of the main findings together with some relevant information from the literature follows.

Identity

Dosidicus gigas is a member of the family Ommastrephidae placed in the sub-family Ommastrephinae. Diagnostic morphological characters are given by Wormuth (1976).

Distribution and Migration

Dosidicus is an oceanic squid with neritic components. It is found in the eastern Pacific from 36°N to 26°S and westward to 125°W.

Areas of high density exist from 0° to 18°S and from 16°N to 28°N, including the Gulf of California (Nesis, 1970; Suda, 1973; Sato, 1976; Wormuth, 1976). The population inhabiting Mexican waters migrates in and out of the Gulf of California most probably in response to feeding and spawning activities. Migration into the Gulf is initiated in January, reaching its northernmost position (29°N) by April. From May to August the stock is found mainly in the upper central section of the Gulf. Starting in July it extends towards the eastern side. Toward the end of August and into September the stock migrates back towards the entrance of the Gulf. At the entrance it separates into two components, one migrates south along the mainland coast and the second extends around the tip of Baja California Peninsula.

The species follows a diel vertical migration which is a common feature in ommastrephids (Clarke, 1966; Roper and Young, 1975).

The Fishery

Fishing for Jumbo squid in the Gulf of California started in 1974, with the operation of a small artisanal fleet working seasonally. Beginning in 1978 the off-season shrimp fleet entered the fishery. In 1979, large Japanese jigging boats commenced fishing. The increase in fleet size coupled with changes in national squid buying policies brought about an explosive growth of the order of 440% in total landings in 1980. Yearly production is given in Table 1.

The fleet has been divided into six categories depending on size of vessels and mode of opera-

[1] Summary of a paper to be published by FAO.

TABLE 1

Year	1974	1975	1976	1977	1978	1979	1980
Catch (metric tons)	14.0	43.4	147.0	300.0	2 000.0	5 000.0	22 000.0

tion, which have direct relation to trip lengths and type of product unloaded. In brief, category 1 comprises open boats, 6-8 m LOA; category 2, snapper boats, 16 m LOA; category 3, shrimp boats, 23-25 m LOA, icing the catch with 20-25 day trips; category 4 shrimp boats, same LOA as category 3, no preservation and daily trips; category 5, small Japanese jigging vessels, 35-40 m LOA; category 6, large Japanese jigging vessels, 48-52 m LOA.

Two types of jigs are commonly used: (a) Japanese type with two steel-hook crowns, 12 cm body size, 12 and 18 mm hook size, and (b) locally built jigs made out of aluminium tube, 30 cm in length and nail crowns as hooks. Japanese jigs are used in combination with automatic or manual jigging machines, as opposed to the local jigs which are used in a one line-one man fashion.

The efficiency of the fleet components was measured relative to the fishing power of the different categories. For this purpose an analysis of variance model derived from the catch equation was used (Robson, 1966). The information analyzed was catch per night operation, for each vessel category working in main squid fishing grounds. Results are shown in Table 2.

TABLE 2

Category	1	2	3	4	5	6
Fishing Power	1.0	1.5	1.5	6.5	11.1	28.0

Similarities between categories 2 and 3 are related to the same number of fishermen fishing with hand lines in boats of different sizes. Differences between categories 3 and 4 are due to differences in operational procedures.

Experiments were performed to evaluate jig efficiencies due to color preferences. Relative jig efficiencies are arranged in descending order: transparent (1.0); red (0.9); pink (0.8); green and silver (0.5). The superior efficiency of transparent jigs is due to bubbles created by holes in the soft plastic body of these jigs. Efficiencies in the other jigs are due solely to colors.

A selectivity study showed that small individuals are caught equally well by both small and large jigs. Large individuals, though still caught with small jigs, are caught in fewer numbers because the smaller hooks do not hold the weight of larger squids (Figure 1). However, in the 12 to 47 cm ML range capture rates with small Japanese jigs and large locally built jigs are the same. Jig selectivity for Jumbo squid is thus a function of the ability of the hook size to retain weight rather than a function associated with jig body size.

Food and Feeding

Most authors agree that *D. gigas* is an active predator at all stages of its life, attacking almost any prey available. The diet is size dependent (Fitch, 1968). Qualitiative analyses of stomach contents show that components vary in accordance with prey species available in different areas (Fitch, 1968; Nesis, 1970; Sato 1976). Jumbo squid in the Gulf of California feed mainly on sardines (*Sardinops sagax caerulea*). In areas of intensive fishing it has been shown conclusively that Jumbo squid are cannibalistic especially on those individuals that have been badly wounded after escaping jigs. The large percentage of empty stomachs observed is due to a very high digestion rate rather than a lack of prey species, which are abundant in the area.

Sexual Maturity

Very little is known about the reproductive cycle of *D. gigas*. Off Chile and Peru, size of first maturity is 20-25 cm ML for males and 36-37 cm ML for females (Nesis, 1970). In the Gulf of California size at first maturity for males occurs when individuals are between 18 to 25 cm ML. Females first mature when they are 35 to 40 cm ML. In males the number and size of spermatophores increase as a function of age and size.

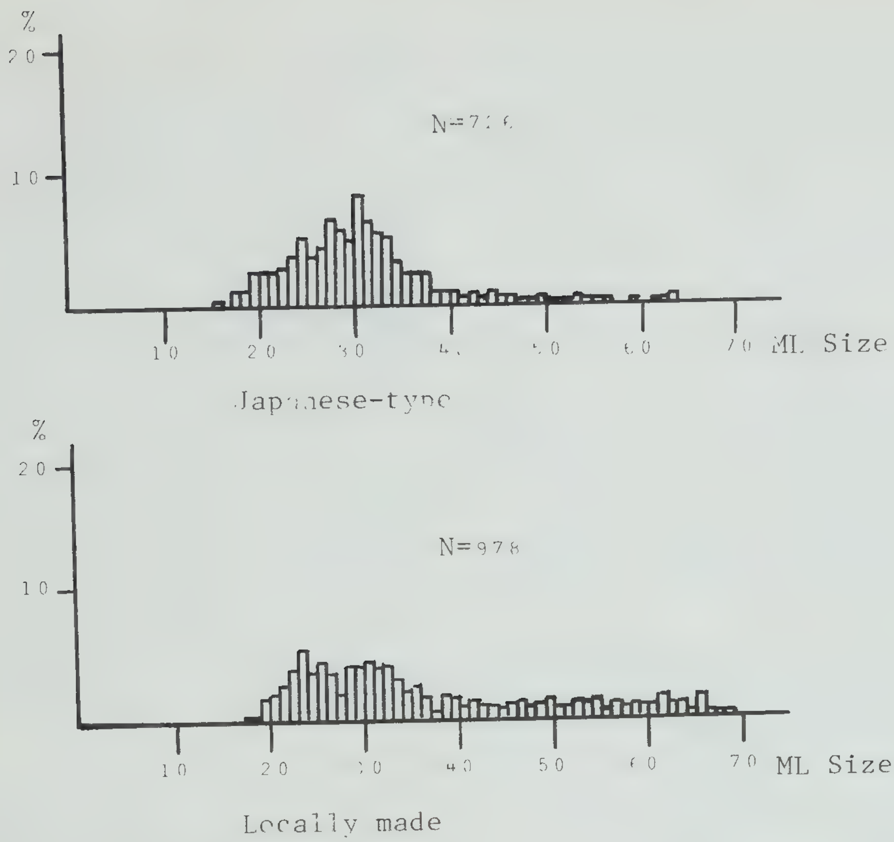


Figure 1. Size frequency distribution for squids caught with Japanese type jigs and large locally made jigs.

Studies of maturity in the Gulf of California show several spawning periods. The most important occurs during December-January, recruiting to the fishery during March and April. A second spawning period occurs in May and June that will recruit in September. A third peak is observed in September whose progeny will recruit in January and February. Mature females are found during most of the year. Three major spawning areas have been defined, one in the eastern central and another in the western central part of the Gulf. A third area is found off the Gulf at the edge of the continental shelf west of the Baja California Peninsula.

The reproductive cycle is not easily defined and appears to be heavily dependent on oceanographic conditions of the area.

Age and Growth

Aging of cephalopods is difficult since few hard parts are found which show annual or other time-related signals. Age and growth estimates for *D. gigas*, given by Nesis (1970) are 20-33 cm for one year old squid, 34-45 cm for two year old and more than 46 cm for three and four year old individuals. Nesis calculated monthly growth rates as 2-2.5 cm during the first year of age and 1-1.2 cm for the second year.

Growth rates for other ommastrephids have been given by Fridriksson (1943), Murata and Ishii (1977), and Araya (this volume).

Maximum size for *D. gigas* varies according to latitude and hemisphere (Berry, 1912; Clarke, 1966; Garcia-Tello, 1965; Nesis, 1970; Phillips, 1961; Wormuth, 1976).

Age and growth studies for the species in the Gulf were conducted with information on monthly mantle length frequency distributions and analysis of the polymodal distributions was

as proposed by Yong and Skillman (1975). The average sizes of the growth components separated by the above method were fitted to a simple von Bertalaniffy growth function, adjusting the function as close to zero as possible in order to assign age to the average lengths previously obtained.

Five different cohorts were defined by the analysis. Growth equations for each one of them are given below:

Cohort	Growth Equation	Birth Date
1	$L_t = 91.98(1\text{-}\exp(-0.12904\ (t+0.291)))$	September
2	$L_t = 11.08 + 4.62\ t$	October
3	$L_t = 99.91(1\text{-}\exp(-0.08133\ (t+0.229)))$	January
4	$L_t = 6.94 + 5.58\ t$	December
5	$L_t = 152.26(1\text{-}\exp(-0.05453\ (t+0.361)))$	March

Each cohort has a different growth pattern depending on its birth date, thus reflecting the effect of varying environmental conditions on growth. Cohorts 2 and 4 grow linearly while the others tend to reach an asymptote. The value of $L_\infty = 152.26$ cm for cohort 5 is unrealistic and is due to a flattened, almost linear growth of the cohort. As such the model in this case is valid only for the range of observed lengths (<50 cm ML). Maximum observed mantle length for all cohorts was 75 cm. In this way, L_∞ values for cohorts 1 and 3 are considered reasonable.

Monthly growth rates from the above functions and for each cohort are presented in Table 3.

TABLE 3

Cohort Age (Months)	1	2	3	4	5
	Growth Rates (cm/mo)				
1- 4	8.33	4.62	6.52	5.58	7.11
5- 7	5.29	4.62	4.90	5.58	5.87
8-10	3.59	4.62	3.84	5.58	4.99

The above growth rates define *D. gigas* as a very fast growing animal as compared with other oceanic ommastrephids. From these same growth patterns it is evident that this species does not live more than 18-20 months.

Length-weight relationships obtained for different body weights as function of mantle length (ML) are given below:

$$W \text{ total} = 0.02646165(\text{ML})^{2.989379}$$
$$W \text{ mantle} = 0.01775312(\text{ML})^{2.940475}$$
$$W \text{ mantle} + \text{head} = 0.02503828(\text{ML})^{2.937908}$$

The exponents suggest isometric growth.

Stock Analyses

Three methods have been utilized to assess stock size and exploitation levels. These are: De Lury (1947) estimates adjusted by Braaten (1968) method; cohort analysis using a backward solution of the catch equation as proposed by Murphy (1965); and yield per recruit analysis using the expanded version of Paulik and Gales (1964).

Population estimates and catchability coefficients by cohorts estimated from the De Lury method are given below (Table 4). Catch per unit of effort values for cohort 2 followed a very erratic trend, so it was not included in the analysis.

TABLE 4

Cohort	Initial Population (No) In Numbers	Catchability Coefficient (q)
1	954 297	0.00008
3	2 359 185	0.00010
4	3 707 255	0.00011
5	1 121 339	0.00023

A t-test showed no significant differences at the 95% confidence level between q-values, implying that each unit of effort was catching the same fraction from each of the cohorts.

Population estimates for all cohorts combined, estimated from cohort analysis are shown in Table 5.

Maximum biomass occurs during May and June while maximum fishing effort which is dephased one month from the optimum occurs during June and July (Figure 2). Likewise, months of maximum effort correspond to population sizes which represent 45.6% and 24.3% of the initial population, whereas during May the population available to the fishery represents 72.6% of the initial population.

Fishing mortality rates (F) averaged over the

TABLE 5

Month	Total Population In Numbers	Total Population Biomass (kg)	Total Catch In Numbers	Total Catch Biomass (kg)
Jan	9'611 908	1'314 406	48 561	147 044
Feb	8'861 166	3'320 603	73'793	104 233
Mar	8'146 654	6'608 266	260 259	340 618
Apr	8'389 552	10'523 260	679 211	974 407
May	6'974 903	13'573 404	1'475 194	1'902 177
Jun	4'386 115	12'544 727	3'170 190	5'559 013
Jul	2'337 707	10'563 121	1'696 567	6'895 828
Aug	1'327 342	7'804 480	685 027	3'448 183
Sep	1'038 585	7'222 269	487 495	2'349 602

period of maximum effort by cohorts are: cohort $1=0.28$; cohort $2=0.22$; cohort $3=0.39$; cohort $4=0.60$ and cohort $5=1.35$.

Yield per recruit analysis was performed with growth parameters for cohorts 1 and 3, defined as the most representative for the species. M-values used were 0.05 and 0.08, a range considered to include the real natural mortality rate. From Figure 3 and at specific values of F as estimated from cohort analyses, it is possible to conclude that at the 1980 fishing effort level the cohorts were exploited at the optimum biological level. Since the fishery acts on a multicohort stock, management schemes by independent cohorts are impossible. An alternative could be to manage it in terms of the less productive cohorts or a combination of cohort abundance and cohort production.

Finally, changes in the environment may greatly affect the availability of this oceanic species in the restricted areal distribution within the Gulf of California. Thus, management schemes should not only consider quantity of investment but also the type of fishing technology to be used in this highly dynamic stock.

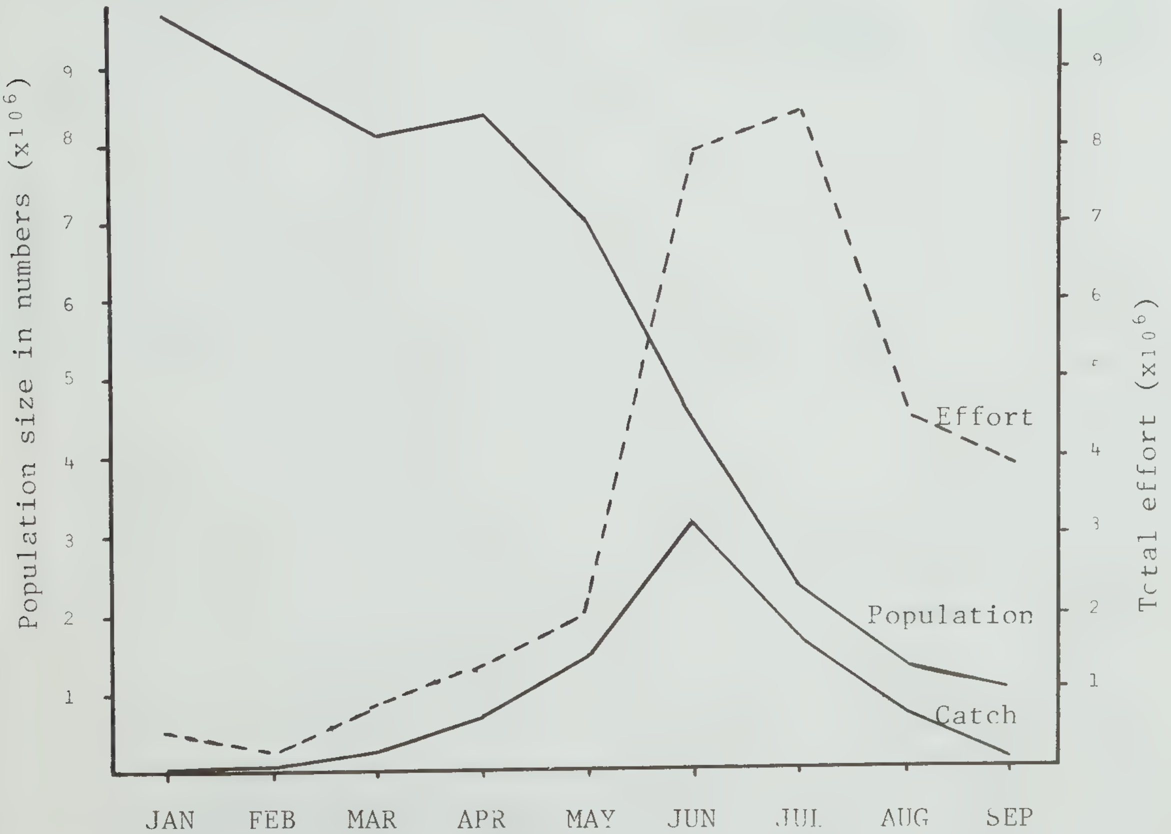
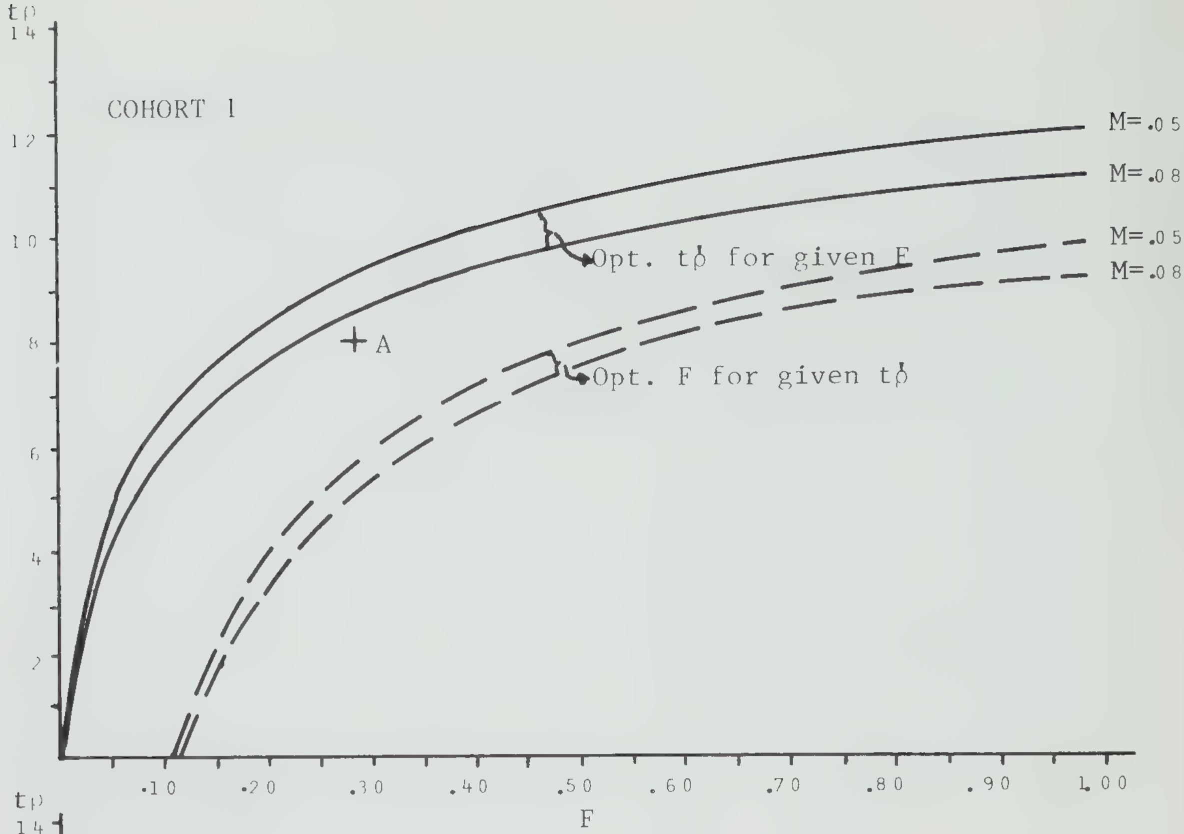


Figure 2. Estimated population size, catch and effort from January to September 1980.



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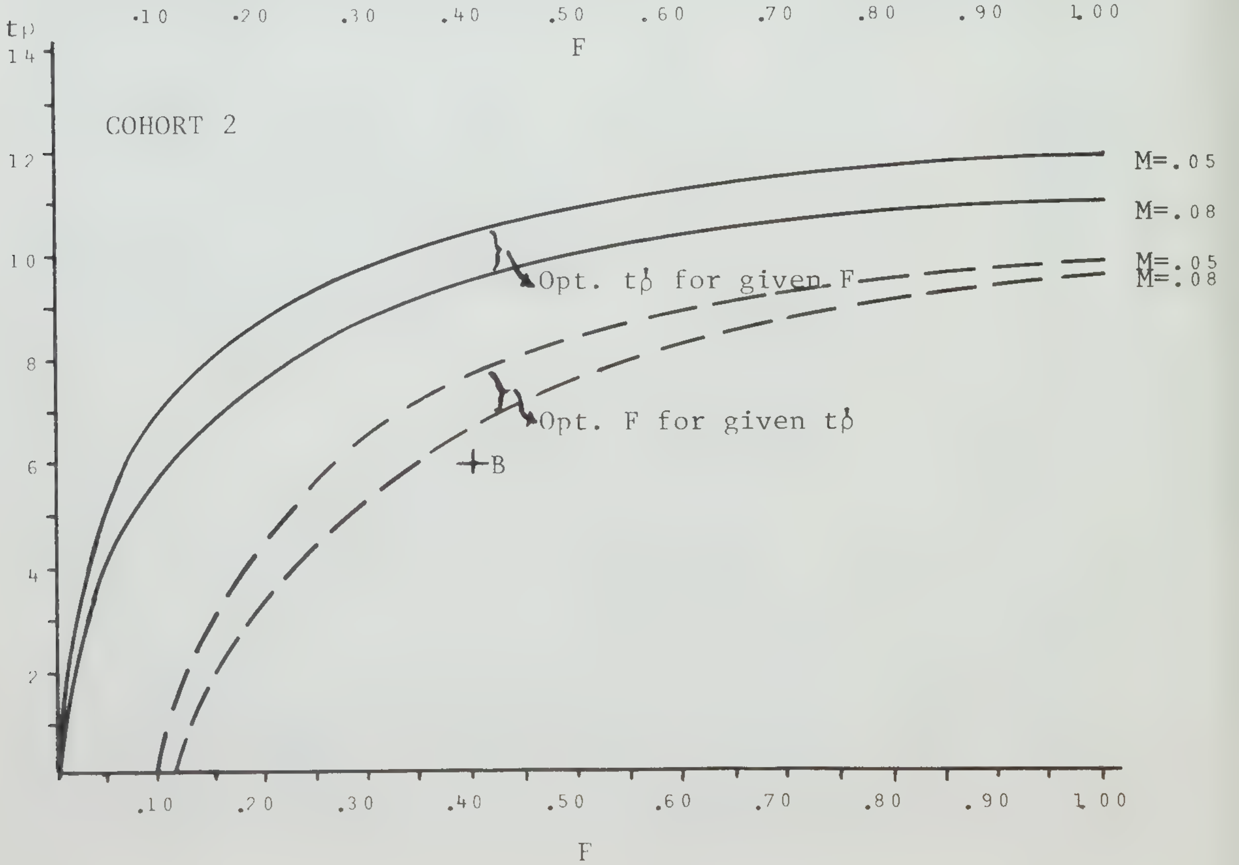

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Opt. F for given tρ
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Figure 3. Eumetric lines showing maximum yield per recruit at various levels of M, F and age of recruitment, $t'\rho$, for cohorts 1 and 3. Points A and B show actual position of cohort exploitation.

Ento